

Nevertheless, the commonly accepted range of some of our most familiar ferns is much more extended than is usual in the case of Phanerogams, and not infrequently is quite at variance with the laws of distribution which have been worked out for the latter type of plants.

In a recent examination of the ferns of the Selkirk Mountains it occurred to the author to make a critical study of some of the forms which are supposed to have a very wide and somewhat anomalous range. It appeared that, in the treatment of closely related species of ferns, and of races within the species, too much reliance had been placed on such superficial characters as details in the form and cutting of the fronds, characters of a kind which botanists have found to be peculiarly unreliable in most groups of plants. It seemed that a study of such technical characters as the size, form and sculpture of the spores, and details of the structure of the sporangia, sori, indusia and scales, might reveal characters of a more stable nature than the purely vegetative ones usually employed. As will be seen in the following series of papers, this study has led, in the case of several of our common groups of ferns, to the separation of species and varieties, in other cases to the recombination of forms supposed to be distinct, and the races characterized by the same technical characters have been found in all cases to have geographical ranges quite in harmony with well-known laws of the distribution of flowering plants.

I. THE GENUS *ATHYRIUM* AND THE NORTH AMERICAN FERNS ALLIED TO *ATHYRIUM FILIX-FEMINA*.

1. THE GENUS *ATHYRIUM*.

Fern genera are traditionally unsatisfactory, and in no part of the group are they more so than in the alliance of which the lady fern is a member. These form a naturally compact group in which it is sometimes difficult to distinguish clearly between the species, yet in some treatments of the ferns the species described below have been relegated to as many as three different genera, while *Athyrium Filix-femina* itself has been placed by reputable authors in at least four of the larger fern genera. This is largely due to the attempt, current throughout the latter part of the eighteenth, and much of the nineteenth century,

to rely entirely upon the structure of the sorus and indusium for generic distinctions and delimitations. This attempt is now seen to have resulted in an artificial system entirely comparable to the Linnaean system of classification of flowering plants. In some cases, particularly in highly specialized groups, it resulted in bringing together related forms, but it often led to obvious absurdities both of aggregation and of separation. It naturally resulted in particularly illogical results in such a group as *Athyrium*, where the sorus is a peculiarly variable and unstable organ.

The genus *Athyrium* Roth ex Mertens¹ was originally founded entirely upon soral characters which further investigation has shown to be illusory. In view of this it is not strange that botanists like Mettenius and Hooker should have found it impossible to maintain the genus, and should have considered it merely as a section of *Asplenium*. In 1866 and 1870, Milde, however, in two notable papers² showed that the lady fern and its relatives differ in several respects from the true *Asplenium*, and refounded the genus *Athyrium* on a firmer basis. He laid particular stress on the structure of the scales in the two genera and on differences in the vascular structure of the frond. He also pointed out that *Phyllitis* (*Scolopendrium*) and *Camptosorus* agree with *Asplenium* in both of these respects, while *Diplazium*, several of the other genera of *Asplenieae*, and the more primitive genera of the *Aspidieae* agree with *Athyrium*. In his second paper he confirms his earlier results so far as the differences between *Athyrium* and *Asplenium* are concerned, but he confesses that he is unable to maintain any generic difference between *Athyrium* and *Diplazium*, and he accordingly transfers a long list of species from the latter genus to *Athyrium*.

In general, the distinctions pointed out by Milde hold very well,

¹ Auszug eines Briefes von Hrn. Prof. Mertens in Bremen an den Herausgeber, Römer's Archiv für die Botanik, ii. pt. 1, 105 (1799).

Roth, A. G., Tentamen Florae Germanicae, iii. 58 (1800).

Roth's diagnostic character was the recurved sorus. Though his description of the genus was evidently based almost wholly on *A. Filix-femina*, which has since been considered the type of the genus, and on its various European forms, which he treated as distinct species, he listed as the first species *A. fontanum*, a genuine *Asplenium* with no close affinity to the lady fern. This species often has some of its sori recurved, and rarely has a few of them hooked as in true *Athyrium*. Roth's reason for placing this fern first was evidently merely that he was arranging all of the species in order, with the least compound first. That he did not consider it typical is evident, as it differs in several respects, notably in its entire indusia, from his generic description.

² Milde, J., Das Genus *Athyrium*. Bot. Zeit. xxiv. 373 (1866).

Id., Ueber *Athyrium*, *Asplenium* und Verwandte, Bot. Zeit. xxviii. 329 et sqq. (1870).

though there are a very few species of *Diplazium* in which one or the other breaks down. Such partially intermediate species occur, however, throughout the ferns, and any attempt to unite the larger fern genera on such grounds would result in reducing such a family as the *Polypodiaceae* to a very few genera — possibly to a single genus.

The scales of *Asplenium* consist of oblong cells, apparently nearly square in cross section, and the vertical interior cell-walls are dark colored and much thickened, while the superficial and marginal walls are very thin and transparent. This gives the scale, under the microscope, a clathrate appearance. In *Athyrium*, on the other hand, the typical scales are composed of elongated, more or less fibrous cells which are somewhat rounded in cross section, and all parts of the cell-wall are equally thickened, sometimes slightly, sometimes very greatly.

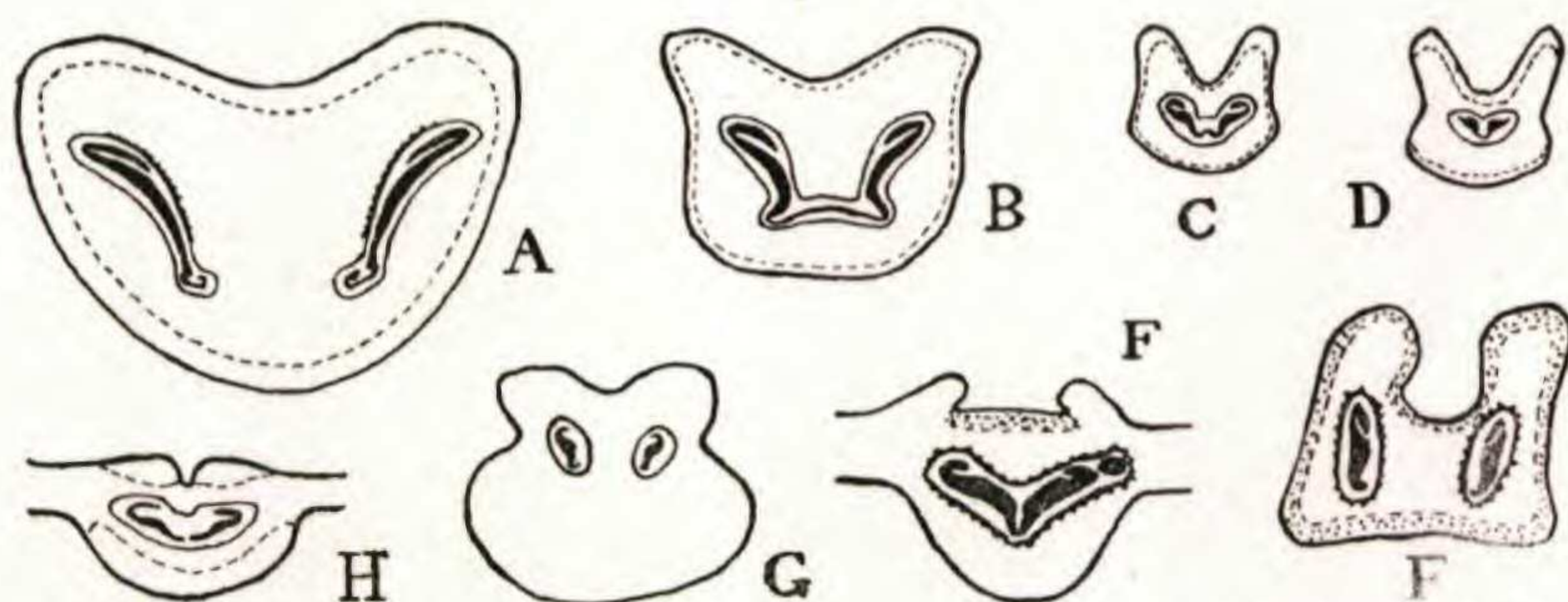


Fig. 1. Structure of the stipe in the genera *Athyrium* and *Diplazium*. A-D, *Athyrium angustum* (Willd.) Presl. A, lower part of the stipe, $\times 5$; B, upper end of the stipe, $\times 5$; C, rachis of the frond; D, midrib of a pinna, $\times 10$; E, F, *Diplazium plantaginifolium* (L.) (Brazilian material). E, stipe, $\times 10$; F, midrib of the blade, $\times 10$; G, H, *D. grandifolium* Sw. G, stipe, $\times 10$; H, midrib of the blade, $\times 10$.

The result is that, under the microscope, there is no such contrast between walls and lumina as is seen in the scales of *Asplenium*. Similar scales are found in *Cystopteris*, in *Dryopteris*, in *Diplazium* and in several other genera. In some species of *Athyrium* and in many species of *Diplazium*, the much reduced scales which occur along the rachis and veins of the frond, and especially in the axils of the pinnae, are somewhat clathrate, but the large basal scales, occurring on the rhizome and on the bases of the stipes are of the characteristic form just described.

In *Athyrium* and *Diplazium* the structure of the stipe and the rachis is rather uniform (see fig. 1). Two large bundles enter the base of the stipe. These may be nearly parallel, but more commonly they are somewhat inclined towards each other on the ab-axial

side of the stipe. They are usually well separated from each other and in a frond broken off at the base, they often project as two perfectly distinct fibrous cords. Taken as a whole, the xylem groups of the bundles are somewhat concave on their inner faces, though their central portion usually curves in the opposite direction. The tips of the xylem groups, and especially those facing the ad-axial side of the stipe are always sharply inflexed towards the middle of the stipe. These inflexed tips of the xylem may extend in at a sharp angle to the main mass of the xylem, in which case they are very conspicuous, or they may be completely inflexed, so as to lie closely applied to the inner face of the main xylem mass. Milde noted the existence of these inflexed parts of the bundle in those ferns in which they are conspicuous, but he seems to have overlooked the entirely parallel condition

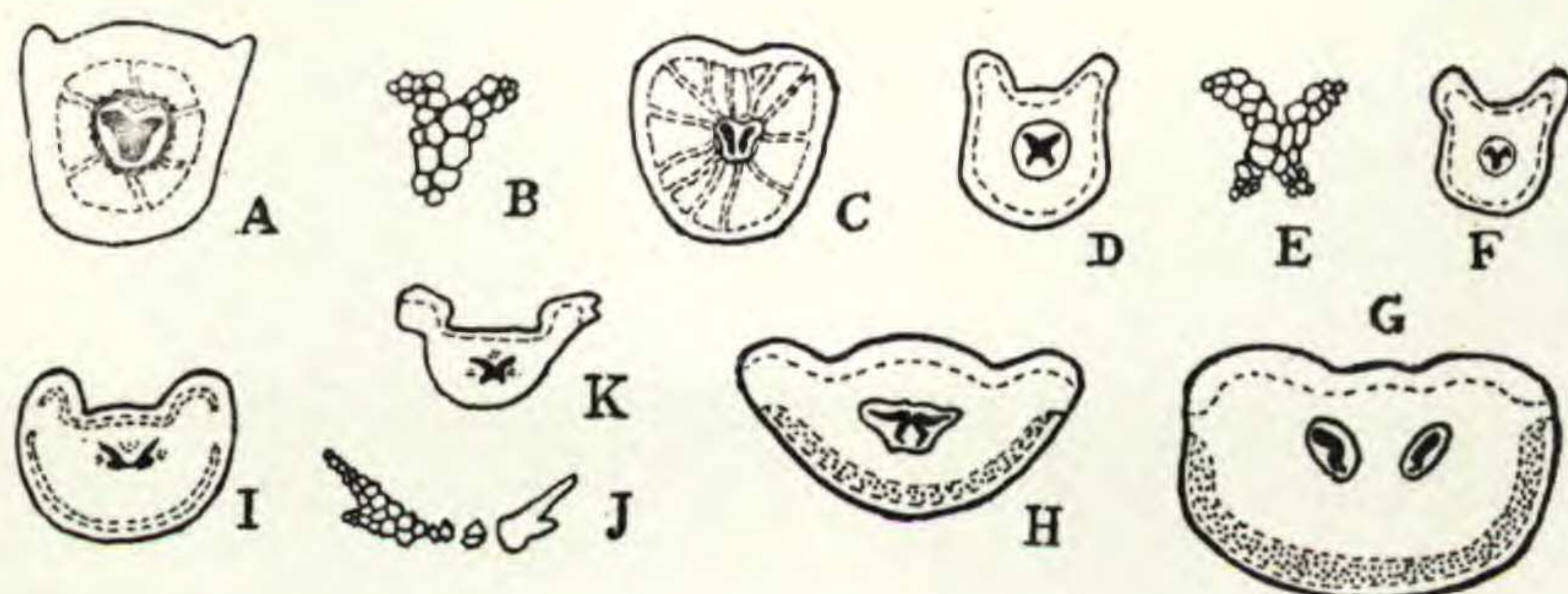


Fig. 2. Structure of the stipe in the genus *Asplenium*. A, B, *A. Trichomanes* L. A, stipe, $\times 10$; B, detail of the xylem of A. C-F, *A. viride* Huds. C, base of stipe, $\times 10$; D, upper part of the stipe, $\times 10$; E, detail of the xylem of D; F, rachis of the frond, $\times 10$; G, H, *A. bulbiferum* Forst. G, stipe, $\times 3\frac{1}{2}$. H, rachis of the frond, $\times 3\frac{1}{2}$. I-K, *A. fragrans* Sw. I, stipe, $\times 2\frac{1}{2}$; J, detail of the xylem of I; K, rachis of the frond, $\times 5$.

in such species as *Athyrium Filix-femina* in which the tips of the xylem are so much inflexed as to be almost hidden against the mass of the bundle. Sooner or later the two bundles unite by their dorsal extremities into a single U-shaped, or rarely V-shaped bundle. The structure of the stipe of *Dryopteris Thelypteris* (L.) A. Gray, *D. montana* (Vogler) Watt and other related species of *Dryopteris* is identical with that of *Athyrium*.

In *Asplenium* the vascular structure of the stipe is less uniform, and Milde recognizes four classes of structure in this genus, besides certain anomalous cases (see fig. 2). There are two small, centrally located bundles, which may be free throughout the length of the stipe and rachis, or may be united above, or even throughout.

When separate, they are more or less crescentic, with the convex side facing towards the middle of the stipe. The ad-axial tips of the bundles are never inflexed. When the two bundles are united, the compound bundle is usually X, Y, or T-shaped. Very rarely, as in *Asplenium fragrans* Sw. (*A. mexicanum* Mart. & Gal.) and *A. bipartitum* Bory (*A. auritum* Watt), the compound is V-shaped, but even then it is not entirely like that of *Athyrium*. Thus we find that in *Asplenium fragrans*, the compound bundle is formed, not by the union of the true ab-axial extremities of the component bundles, but by the junction of the points of narrowly V-shaped bundles (I and J, fig. 2).

There are certain minor points in which *Asplenium* nearly always differs from *Athyrium* and *Diplazium*. In the first mentioned genus, the walls of the sclerenchymatous cells of the stipe have a distinctly red color,—it is this which gives the characteristic red-black hue to the stipes of many species of *Asplenium*. In *Athyrium* and *Diplazium* on the other hand, the sclerenchymatous cells of the stipe have yellow or yellow-brown walls. A similar difference obtains in respect to the thickened walls of the cells of the scales.

In *Asplenium* the veins of the ultimate segments tend to be repeatedly dichotomous, while in *Athyrium* and *Diplazium* the veins are pinnate, and the veinlets are either simple or once forked. Very rarely indeed in these genera is a vein forked twice.

The distinctions between *Athyrium* and the genera *Diplazium* and *Dryopteris* are based entirely on the character of the sorus. As has already been stated, this organ in *Athyrium* is very variable and in many species two, or even three distinct types of sorus occur, even on the same frond. The simplest of these types from the descriptive stand-point, though almost certainly not the most primitive, is that which is characteristic of the genus *Asplenium* (see fig. 3). Here the sorus extends for a greater or less distance along the anterior side of a vein,¹ and is covered by an indusium, which grows out from the

¹ When the subtending vein is forked or otherwise branched, the primary sorus occurs on the anterior side of the anterior branch of the vein. Secondary sori may occur on the posterior side of the anterior branch, and the anterior side of the posterior branch, and in corresponding positions on the other branches if there are any. It is to be noted that the secondary sori are always on the anterior side of the veinlets, if we consider their orientation in regard to the group of veinlets, viewed as an ultimate segment of the frond, rather than in respect to the segment of the next lower order, which controls the position of the primary sorus. As has been pointed out by E. J. Winslow (Double Sori in *Athyrium*, Am. Fern Journ. iii. 88, 1913), it is at such points of confused and indeterminate orientation that diplazioid and athyrioid sori especially tend to develop.

subtending vein and lies upon the sporangia. In the genus *Athyrium* such sori seem always to be in close contact with the subtending vein throughout their entire length, and never, as in some species of *Asplenium*, to curve away from it at the ends. Asplenioid sori vary greatly in length, but are otherwise quite uniform in character. The indusium is raised and pushed back by the developing sporangia, and at maturity is often completely reflexed.

The sorus characteristic of the great tropical genus *Diplazium* and found also in some species of *Asplenium* and *Athyrium*, consists of two

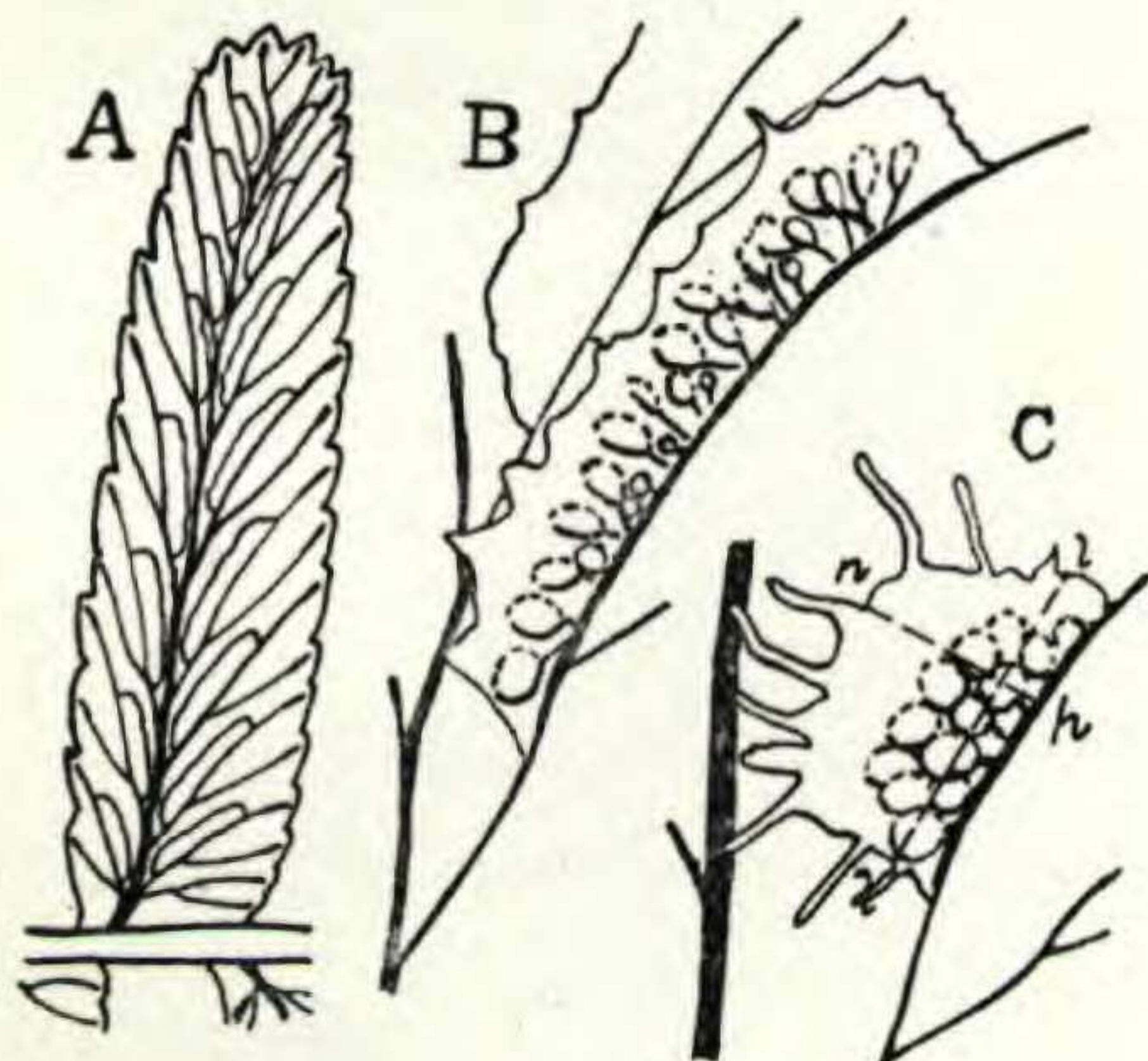


Fig. 3.

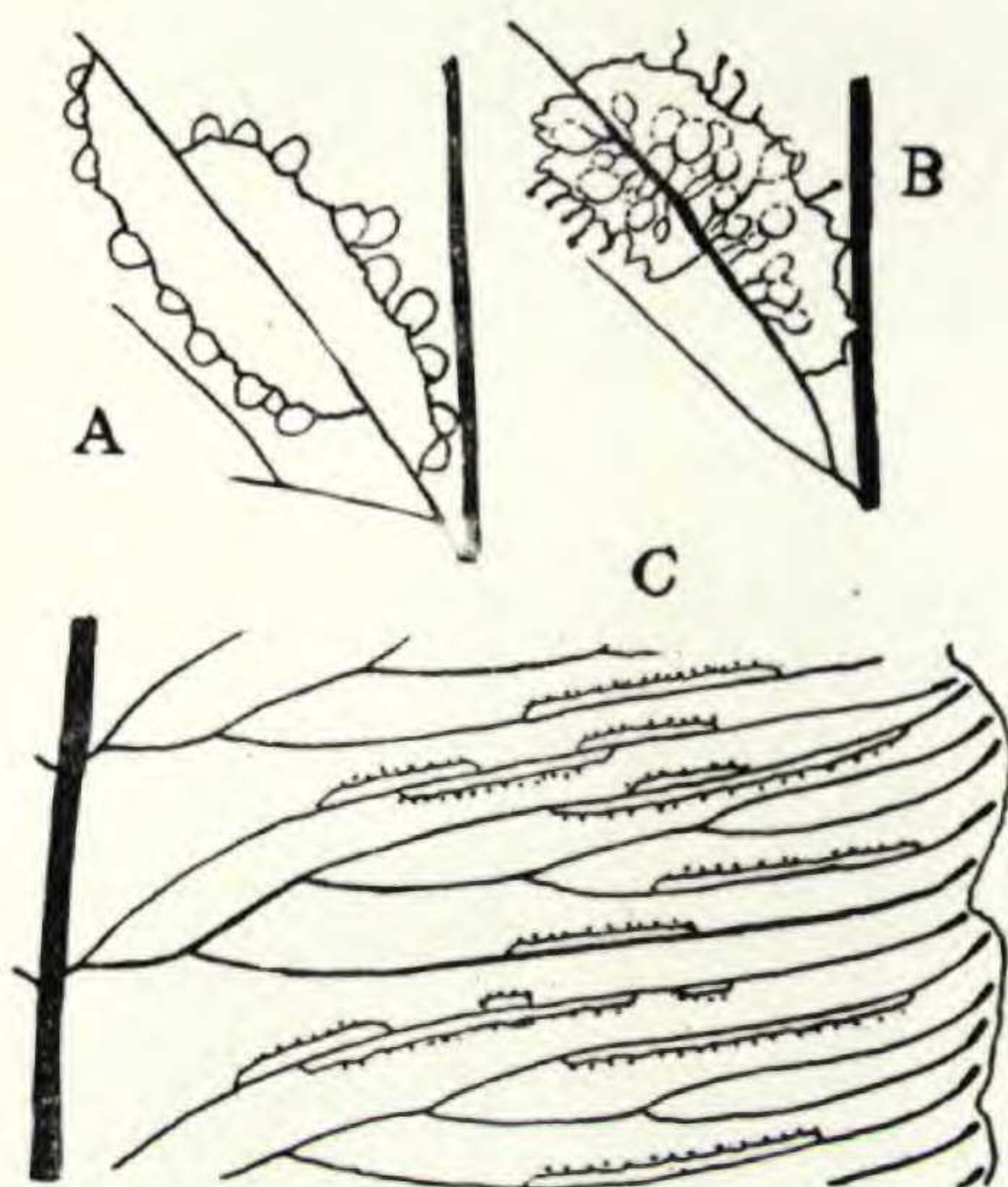


Fig. 4.

Fig. 3. Asplenioid sori. A, B, *Asplenium platyneuron* (L.) Oakes. A, pinna, $\times 2\frac{1}{2}$; B, young sorus, $\times 10$, the sporangia indicated as if seen through the transparent indusium. C, sori from the distal portion of the pinnule of *Athyrium Filix-femina* (L.) Roth., l-l, line measuring the length of the indusium, h-h, line measuring its height.

Fig. 4. Diplazioid sori. A, *Diplazium acrostichoides* (Sw.) Butters, $\times 12\frac{1}{2}$; B, *Athyrium asplenioides* (Michx.) Desv., $\times 12\frac{1}{2}$; C, portion of the frond of *Diplazium plantaginifolium* (L.) Urban, natural size.

asplenioid sori standing back to back along the same vein (see fig. 4). Such sori may vary not only in their absolute length (in some species of *Diplazium* reaching over 2 cm.) but also in the relative length of the component parts. In general, the anterior sorus is longer than that on the posterior side of the vein. In typical *Diplazium* the indusia wither at maturity.

The characteristic athyrioid sorus may be described as an asplenioid sorus which at the distal end crosses the subtending vein (see fig. 5). Athyrioid sori display great diversity of form. At the distal

end, the sorus may barely cross the veins so as to be slightly hooked, a "hamate" sorus, or it may develop a considerable posterior limb, becoming horse-shoe shaped, or "hippocrepiform." In the latter

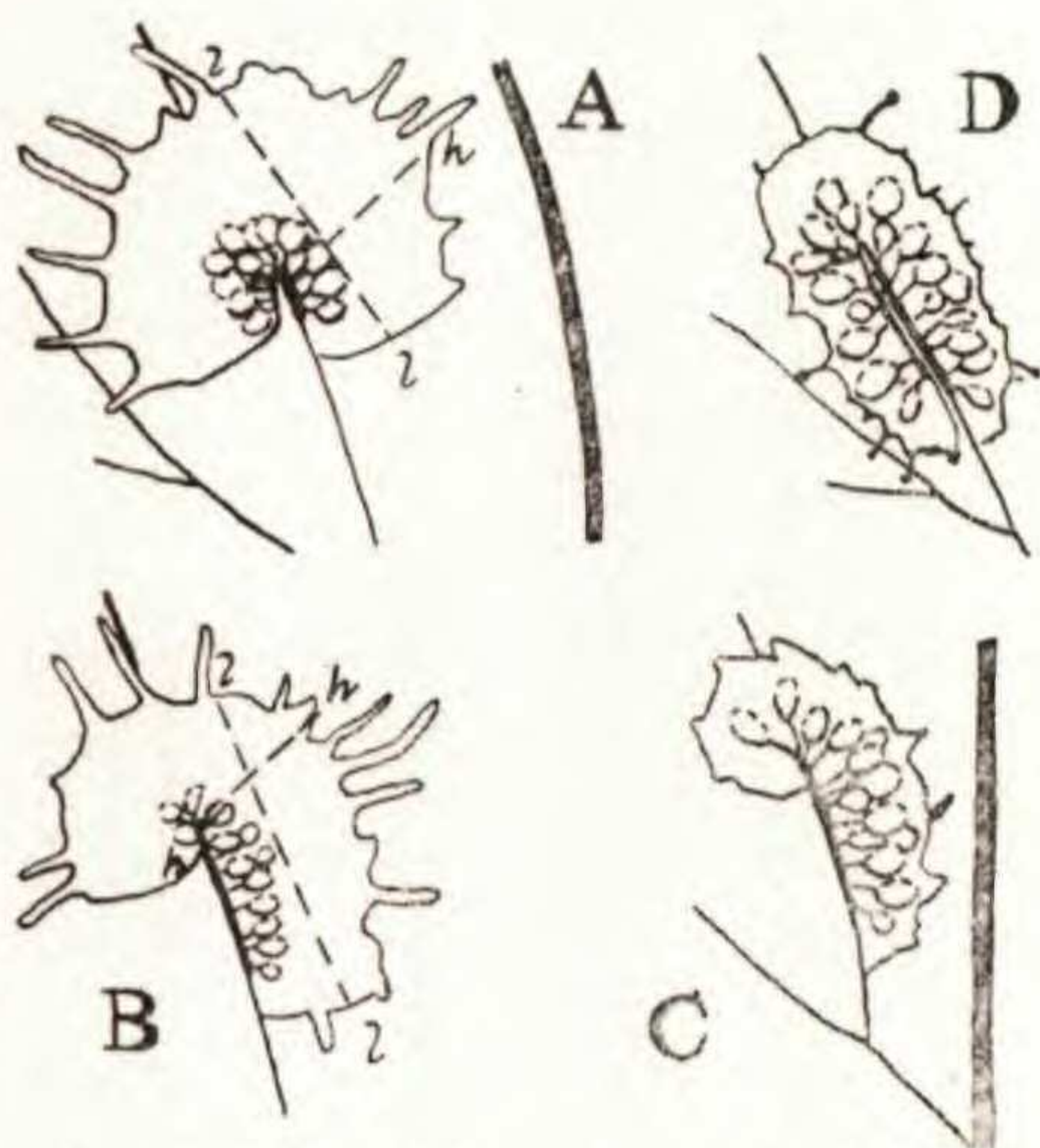


Fig. 5. Athyroid sori. A, B, *Athyrium Filix-femina* (L.) Roth, l-l, length, h-h, height of the indusium. C, *A. angustum* (Willd.) Presl. D, *A. asplenioides* (Michx.) Desv. A and D are hippocrepiform, B and C, hamate.

case the two limbs may lie close together, or the posterior limb may lie at a visible distance from the subtending vein. Moreover, the entire sorus may be several millimeters long, or may be so short as to appear nearly round. In typical *Athyria*, the indusium of the mature sorus is reflexed wherever there is sufficient room, and at the curved distal end, it is crowded up into a vertical position in the midst of the sporangia. It is easy to see that the condition in a very short athyroid sorus is but a brief step from that which obtains in such a fern as *Dryopteris Thelypteris* (L.) A. Gray, in which an essentially round sorus is covered

by a centrally placed indusium shaped like an umbrella, but discontinuous on the proximal side. Finally, in a very short sorus, only that part may be present which crosses the vein, and the indusium may then also merely cross the vein, usually somewhat obliquely and just behind the sorus, a condition very like that found in the genus *Cystopteris*. Cystopterid sori are also fairly common in some of the more primitive species of *Dryopteris*, e. g. *D. Thelypteris* and its allies. In this connection it is interesting to note that Bower¹ considers *Cystopteris* as a relatively primitive type from which the *Aspidieae* have probably developed, and it seems equally probable that *Athyrium*, and through it the other genera of *Asplenieae* have developed from a similar origin.

It is readily seen, that with such variability of the sorus, it is not easy to define the limits of the genus *Athyrium*. In this connection there are two major problems, the limit between *Athyrium* and *Dryopteris*, and the question of the genus *Diplazium*.

¹ Bower, F. O., *The Origin of a Land Flora*, 615 (1908).

As Copeland has well pointed out,¹ *Athyrium* and *Dryopteris* are both relatively primitive genera of *Polypodiaceae*, presumably with a common origin, and between the more undifferentiated species of the two genera there is really no definable difference. In both groups, species occur with small hippocrepiform, round and cystopterid sori mingled on the same frond, and it becomes necessary to judge such cases, each on its individual merits. Thus *Athyrium mongolicum* (Franch.) Diels, which has many cystopterid and dryopterid sori mingled with other athyrioid ones is more closely allied to the *Filix-femina* group of *Athyria*, than to any species of *Dryopteris*, while *Dryopteris Schaffneri* (Fée) C. Chr., with a similar assortment of sori, is obviously a member of the somewhat specialized section *Goniopteris* of the genus *Dryopteris*. Similarly, in one of the species discussed in this paper, *Athyrium alpestre* (Hoppe) Rylands, evidence from the sori is at best very slight, and in some of its forms, as, for example, that found in America, such evidence is entirely wanting, yet, so closely do some of its forms approach to certain forms of the common lady fern, that the two species can scarcely be kept separate, and there can be no question of the generic position of *Athyrium alpestre* in any natural classification of ferns.

In this connection, it is well to note that Christensen² has found the type of pubescence very useful in classifying ferns of the genus *Dryopteris*, and it bids fare to be equally useful in delimiting the groups of the genera *Athyrium* and *Diplazium*, and in indicating the true affinities of certain anomalous species.

In the direction of *Diplazium* the limits of the genus *Athyrium* are even harder to define. As stated above, Milde³ decided finally that this is an impossible task, and he then merged the two genera, while Copeland holds⁴ that the Asiatic *Diplazia* have had a multiple origin from the typical *Athyria*, and therefore cannot properly be regarded as constituting a genus. The Asiatic forms of *Diplazium*, and of *Athyrium* also, are certainly much more complex in their relationships than the American forms, and the final settlement of this question will depend on a careful working out of the lines of evolution of the

¹ Copeland, E. B., A Revision of the Philippine Species of *Athyrium*. Philip. Journ. of Sci. Bot. iii. 285 (1908).

² Christensen, C., On a natural Classification of the species of *Dryopteris*. Biol. Arb. tileg. Eug. Warming (1911).

³ Milde J., Ueber Ath. etc., Bot. Zeit. xxviii. 329 (1870).

⁴ Copeland, E. B., loc. cit.

Asiatic groups. As both of the genera involved are already of considerable size,—according to Christensen's Index, *Athyrium* has 85 valid species, and *Diplazium*, 206,—a merging of them seems undesirable unless it is absolutely required by considerations of taxonomic honesty. So far as American ferns are concerned, the author finds that *Athyrium acrostichoides* (Sw.) Diels shows, in the thickened walls of the cells of its indusium, and in its pubescence, far closer kinship for the ordinary type of tropical American *Diplazium*, than for ferns of the lady fern group, and the same is true of *Athyrium angustifolium* (Michx.) Milde.¹ It seems that it may be possible eventually, to limit the genus *Athyrium* to the lady fern and its immediate allies, and possibly to form two or more genera out of the more remote groups of *Athyria* and *Diplazia*, but careful monographic work upon the whole complex is very much needed at the present time.

Finally it appears that the contact between these ferns and the true *Asplenium* is through once pinnate (or possibly entire leaved) tropical forms such as *Diplazium semihastatum* (Kze.) C. Chr. and *Asplenium bipartitum* Bory, as it is only among ferns of this general type, that any forms with intermediate vascular structure occur. While the larger, 2–3 times compound *Asplenium* sometimes closely simulate certain species of *Athyrium*, the structural differences are always perfectly sharp and clean cut.

The close resemblance of the western ferns commonly classified as *Athyrium cyclosorum* to certain European forms of *A. Filix-femina*, led to an examination of all the American and old world material of these species in the Gray Herbarium. From this examination certain conclusions were reached, which are discussed at length below. These conclusions are as follows:

1. That in the eastern United States and Canada there are two distinct species of lady ferns, neither of which is conspecific with *A. Filix-femina* (L.) Roth of Europe. One of these two species, *A. asplenoides* (Michx.) Desv. is prevailingly southern in its distribution, the other, *A. angustum* (Willd.) Presl, is prevailingly northern.

2. That the ferns of the northwest are conspecific with the Euro-

¹ In the opinion of the author these ferns should be known as ***Diplazium acrostichoides*** (Sw.), comb. nov. (*Asplenium acrostichoides* Sw. Schrader's Journal 1800, ii. 54 (1801), *Asplenium thelipteroides* Michx., Fl. Bor.-Am. ii, 265 (1803), *Diplazium thelipteroides* Presl, Tent. Pterid. 114, 1836) and ***Diplazium angustifolium*** (Michx.), comb. nov. (*Asplenium angustifolium* Michx., Fl. Bor.-Am. ii, 265, 1803).

pean plant, but, in some cases, differ from the common European forms of *A. Filix-femina* in certain minor points, and are then best regarded as a geographical variety of that species.

3. That the lady ferns of California, and the southern Rocky Mountains differ more markedly from the European plant, but are not clearly distinct from the more northern form, and therefore are best considered as a second, and much more aberrant geographical variety of *A. Filix-femina*.

4. That a boreal and high alpine fern found in eastern Quebec and in the alpine areas of western North America, is a clearly distinct geographical variety of the old world *A. alpestre*.

2. *ATHYRIUM FILIX-FEMINA* (L.) Roth.¹

Since the conception of this species among American botanists seems to have become considerably confused by the failure to distinguish it from the related forms of eastern America, a brief account of its chief characteristics seems desirable. The following description has been drawn up mainly from the specimens of the European plant in the Gray Herbarium (about twenty-five in number), together with a careful comparison with the standard works on British and continental ferns.

The rhizome is generally described as erect, sometimes as erect or ascending, rarely as decumbent. Even in cases where it is not entirely erect, there appears to be always, a distinct upright crown of fronds, with the young growth in their midst.²

¹ *Polypodium Filix femina* L. Sp. Pl. ii. 1090 (1753). *Athyrium Filix Foemina* Roth ex Mertens, Archiv für die Botanik, ii. pt. 1, 106 (1799). *Athyrium Filix femina* Roth, Tent. Flor. Germ. iii. 65 (1800).

² The character of the rhizome is in general poorly shown in herbarium material. In the Gray Herbarium only two European plants of this species show the crown of the rhizome. One of these from Holstein, has the rhizome ascending at an angle of about 70°, the other, from Saxony, at an angle of about 45°. An Algerian specimen has the rhizome ascending at an angle of about 60°, and curving upward. In all these specimens the young growth is surrounded by the bases of the older fronds.

In this connection the testimony of certain European writers is interesting. Thus Newman, Hist. of Brit. Ferns, ed. I. 62 (1840), says "The Rhizome is vertically elongate, sometimes rising several inches above the surface of the ground: in one instance I have seen it more than a foot in height, thus evincing a considerable proximity to the *Dixoniae*, and other tree ferns," and Moore, Popular History of British Ferns, ed. I. 87 (1851), states, "The habit of the plant is tufted, the caudex of the larger varieties often with age acquiring some length, and elevating the circlet of fronds on a low, rude pedestal; this stem, however, never acquires more than a few inches in length. In winter, the summit of this stem, whether a tuft seated close to the ground, or elevated a few inches above the surface, is occupied by a mass of incipient fronds, each rolled up separately, and nestling in a bed of chaffy scales," while Milde, Die Gefäss-Crypt. Schles. 570 (1858), speaks of the "ganz aufrechten oder wenig aufsteigendem Rhizome."

The crown of the rhizome and the lower one-third of the stipes are covered rather densely, and the upper portions of the stipes more sparingly, with large rather persistent scales. These are sometimes over 1 cm. long, and up to 3 mm. wide, lanceolate, and contracted to a narrow base, so that in falling one leaves a very small scar which is almost round or like a minute inverted U. The scales are translucent and glossy, so that it is difficult to evaluate their true color. Seen against a white background, e. g. an herbarium sheet, they generally correspond to the "tawny" or "russet" shades of Ridgway's Color Standards, Plate 15. Very rarely they are darker, approaching Ridgway's "Mars Brown." The cells of which they are composed are large enough to show plainly with a hand-lens of moderate power, and under a compound microscope appear as elongated, but scarcely fibrous cells about six times as long as they are wide.

The stipes are commonly very short, one-fourth to one-third as long as the frond. The fronds themselves are lanceolate, widest in the middle, and tapering about equally in both directions. The lower pinnae are rather remote, in general strongly deflexed, and, though but little reduced in width, only one-fourth to one-half as long as the middle pinnae.

In the details of the arrangement, form and cutting of the pinnules, this species, like all of its close relatives, is very variable, and innumerable "varieties" have been named, sixty five of which are enumerated and described by Moore in his "Nature Printed British Ferns."¹

The sori differ considerably in different specimens, and different parts of the same specimen, but have certain general characters which distinguish them clearly from those of the east American plants of this group (see Plate 123, figs. 1 and 2, also text-fig. 3, p. 175 and text-fig. 5, p. 176). They are uniformly short, very rarely reaching the length of 1 mm. Strictly asplenoid sori are rare, and are usually found only at the distal extremity of the pinnules, where the sori are considerably reduced in size. A very common form is the sorus which runs along the anterior side of the subtending vein for about 0.75 mm., and then crosses it without extending at all down the posterior side of the vein. In many specimens, horse-shoe shaped sori, and even round sori are found. In sori of the latter types, the indusium is

¹ Good figures, showing the general aspect of this fern may be found in the work just mentioned, Folio ed. pl. 30-34, 8vo. ed. pl. 52-66, in Lowe, E. J., Our Native Ferns, pl. 35, also in his Ferns British and Exotic, v. pl. 29, and in Schkuhr, Ch., Kryptogamische Gewächse, pl. 58.

bent sharply back upon itself, with the two sides in contact, so that it stands in the midst of the sporangia of the distal half of the sorus.

The indusia are usually provided with an abundance of long multicellular cilia. These are occasionally rather few in number, and in old sori they often become so shrivelled that they are not easily seen, except with the compound microscope, and after careful dissection. In no specimen examined were they wanting. The average height of the indusia, not including the cilia, is 0.55 mm., and their average length in the larger sori is 0.8 mm.¹ In the case of the short asplenioid sori near the tips of the pinnules the indusium is often higher than it is long. At both extremities the indusium ends abruptly, so that its sides meet the line of attachment nearly perpendicularly, and sometimes it is even contracted towards the base.²

The stalks of the sporangia are short and very frequently proliferate, the branch usually bearing a secondary sporangium. Occasionally the secondary sporangium is abortive, and rarely it is replaced by a glandular structure. In no specimen seen are such glands freely and uniformly produced as they are in nearly all east American material.

The spores are yellowish, sparsely papillate, and average $39.1 \times 24.1 \mu$ in size.

3. THE LADY FERNS OF THE EASTERN UNITED STATES AND CANADA.

In the eastern parts of North America there are two species of the lady fern group which appear to be amply distinct from each other and from the true *Athyrium Filix-femina*. These are *A. asplenioides* (Michx.) Desv. and *A. angustum* (Willd.) Presl. The former is a southern species, ranging from Florida to Texas, and north to Missouri, Indiana, Ohio, and along the Atlantic coast to eastern Massa-

¹ All measurements of indusia in this paper were made upon indusia dissected off from the frond and flattened out under a cover glass. The length is always measured in a straight line, as nearly as possible parallel to the line of attachment of the indusium, the height in a straight line from the attached edge of the indusium to its free margin. See text-figure 3, p. 175, and text-figure 5, p. 176.

² The soral characters of the true *A. Filix-femina* are reflected in the treatment of it by European botanists. Thus Linnaeus, who defined *Polypodium*, "Fructificationes distributae in puncta rotunda, per paginam folii aversam (Gen. Pl. ed. 5, 485, 1754), placed the lady fern in that genus between *P. cristatum* and *P. Filix-mas*, and *P. aculeatum*, *P. rhaeticum* (a mixture of *Athyrium Filix-femina* and *A. alpestre*) and *P. noveboracense*. It has been placed in *Nephrodium* and *Aspidium* and by most recent European botanists in *Athyrium*. Those who, like Mettenius and Hooker placed it in *Asplenium* have held very broad views of the extent and characteristics of the latter genus.

chusetts, the latter is a northern species ranging from Labrador to Manitoba, and southward to southern New England, the mountains of Pennsylvania, the region of the Great Lakes, northern Missouri and the Black Hills. The two species meet chiefly in southern New England.

In both of these species the rootstock is horizontal or nearly so, and the young growth appears at the end, in advance of the bases of the older fronds, instead of surrounded by them as in *A. Filix-femina*. At the same time the two species differ considerably from one another in their underground parts. *A. asplenoides* has the rootstock distinctly creeping, and only partially and incompletely covered by the short persistent bases of the fronds, the whole structure being only 1-1.5 cm. in diameter. The fronds of each season's growth are loosely clustered, and the next season's growth projects conspicuously beyond the bases of the fronds of the current season. *A. angustum* has a much more condensed rootstock completely covered by the long overlapping fleshy persistent bases of the fronds, the whole structure being 2-5 cm. in diameter. The fronds are usually produced in considerable numbers, and as the rootstock grows but slowly, they are bunched together, but not truly tufted or forming a crown as in *A. Filix-femina*. The new growth stands in front of the fronds of the current season, but does not project conspicuously as in *A. asplenoides*.¹

The young growth of *A. asplenoides* is covered with scales which are smaller and proportionally narrower than those of *A. Filix-femina* but similar in color and structure. In the American fern, however, these scales are for the most part quickly deciduous after growth starts, and the stipes and bases of the mature fronds show very few scales, and these commonly of very small size (3-5 mm. long, by less than 1 mm. wide).

¹ I have laid particular emphasis on this point because D. C. Eaton, *Ferns of the Southwest*, U. S. Geog. Surveys West of the 100th Meridian, vi. 330 (1878), says, "Moore separates the greater part of the North American ferns specifically under the name of *Athyrium asplenoides*, Desv., making two varieties, one with broader and one with narrower pinnules, but the distinctive character which he relies mainly upon, the 'creeping caudex,' seems to be invalid, as our American plants grow in crowns no less decidedly than those of Europe." The context shows that Eaton was not confining these remarks to the western ferns, which are truly tufted, but that he entirely ignored the difference between the close crowding of leaves due to a very slow horizontal growth of the rootstock, and the true crown which arises when the growth is vertical or nearly so. Certainly the quotations in the footnote on p. 179 are very far from describing the condition of the rootstock in either of our east American species. It is noteworthy that all European botanists who have been dealing with living American plants in cultivation have noted the difference in the underground parts between these plants and *A. Filix-femina*.

The scales of *A. angustum* are quite different from those of either of the other species just mentioned. They are of moderate size (up to 1 cm. long and 1.5 mm. wide, usually considerably shorter than this). In shape they are narrowly linear-lanceolate with a fairly wide base, and in falling they leave larger and more conspicuous scars than do the wider scales of *A. Filix-femina*. They are much more opaque than those of the last mentioned species, and generally of darker color, varying from the "Mars Brown" of Ridgway's Color Standards, Pl. 15, to nearly black, with the middle often darker than the edges. Under a moderately strong hand-lens it is difficult to make out any structure, while under a compound microscope, they are seen to be composed of narrow fibrous cells about 15 times as long as they are wide.

In the form of the frond, the two American ferns are decidedly dissimilar. *A. angustum* closely resembles *A. Filix-femina*, but its stipes are commonly proportionally longer,—often one-half as long as the fronds,—and the lower pinnae are not quite so much reduced in size, and are less strongly deflexed than in that species.

A. asplenoides has still longer stipes, about equalling the narrowly deltoid lanceolate fronds. The second pair of pinnae are commonly the longest, and the basal pinnae are only very slightly reduced in length.

The details of the fronds of both American species are, as in *A. Filix-femina*, very variable, but the following points are worthy of note: the fronds of *A. angustum* are often markedly dimorphic, the segments of the fertile fronds being much narrower and more acute than those of the sterile fronds; the pinnules of the fertile fronds of *A. angustum* are commonly narrowly lanceolate and acute, those of *A. asplenoides*, oblong or linear-oblong and obtuse (in very large fronds, however, the pinnules may be deltoid-lanceolate and sub-acute, and the segments of the third order oblong and obtuse.¹

In the structure of the sori and indusia, the two east American species are markedly different from *A. Filix-femina* and from each other. The sori in both American species are prevailingly asplenoid and for the most part over 1 mm. in length, those of *A. asplenoides* being longer than those of *A. angustum*. Athyrioid sori are generally

¹ For a discussion of the various forms and varieties of *A. asplenoides* and *A. angustum*, see below, p. 188 et seq. For illustrations of the pinnules of the various forms of these species see Plate 123, figures 3-18.

either long sori, rather sharply hooked at one end (hamate), or else long horse-shoe shaped, while the short and almost round type so commonly found in *A. Filix-femina* is very uncommon. Diplazioid sori are somewhat rare, but are more common than in *A. Filix-femina* (see Plate 123, figs. 4, 6, 11, 13 and 16, also text-figs. 3-5, pp. 175, 176).¹

The indusium of both American species is broadest at the base, and is often markedly decurrent along the subtending vein. The margin of the indusium of *A. angustum* is usually toothed, or furnished with a few short one-celled cilia (Plate 123, fig. 17). Rarely, especially in the later fronds of the season, it has a few longer, multicellular cilia similar to those found in *A. Filix-femina*. The indusium of *A. asplenoides* is ciliate with multicellular hairs which have swollen glandular tips of a yellow-brown color, a character which is conspicuous under the compound microscope in the recently matured indusium, but is sometimes difficult to demonstrate in over mature specimens, in which the cilia are often broken (Plate 123, fig. 8). The indusia of the largest sori in *A. angustum* measure on the average, 0.5 mm. high, by 1.1 mm. long, those of *A. asplenoides* 0.45 mm. high, by 1.3 mm. long. Even the small sori toward the tips of the pinnae never have indusia higher than they are long.

In *A. asplenoides* the stalk of the sporangium bears a yellowish, long-stalked, glandular body (Plate 123, fig. 9). In *A. angustum*, similar glands are common but by no means as uniformly present as in *A. asplenoides*, and sometimes the stalks of the sporangia proliferate and bear secondary sporangia as in *Filix-femina*.

The spores of *A. angustum* resemble those of *A. Filix-femina*; their average size is $38.6 \times 24.7 \mu$. The spores of *A. asplenoides*, on the other hand are furnished with a nigrescent, wrinkled or reticulate exospore, and resemble rather the spores of *A. alpestre* of arctic-alpine Europe and America. Their average size is $36.0 \times 25.5 \mu$ (Plate 123, figs. 10 and 18).

It will be seen, therefore, that the two species of lady ferns of the eastern states and Canada differ from each other and from *A. Filix-femina* in characters of rootstock, scales, fronds, sori, indusia and spores.

The history of the treatment of these ferns by botanists, American

¹ Asplenoid sori in the American species, particularly the rather long ones of *A. asplenoides*, are somewhat curved, or "lunate," with the convex side facing away from the subtending vein. The amount of this curve depends chiefly on the absolute length of the sorus. It is not to be confused with the sharp bend which occurs in athyroid sori.

and foreign, is interesting and somewhat illuminating. Prior to the work of Michaux, no mention is made of the American occurrence of any species of this group. Michaux assigns two species to eastern North America, describing one as "*Nephrodium Filix foemina*," with the habitat "Canada," and the other as "*Nephrodium asplenoides*," with the habitat "from New England to Carolina."¹

The following year, Sprengel² described *Asplenium Athyrium* apparently from slightly different material of the same species which Michaux had called *Nephrodium asplenoides*. He states that he gives it this name because it has the greatest similarity to *Athyrium Filix-femina*, and ends his description, "Ich vermuthe dass dies Michaux *Nephrodium asplenoides* ist." These two names have been treated as synonyms by all subsequent botanists. In 1809, Schkuhr,³ after publishing a description of *Asplenium Athyrium*, with an excellent plate, had a change of heart and added the statement "aber nach andern Beobachtungen an mehrern aus Amerika erhaltenen Exemplaren kann ich solchen jetzt von *Aspid. Filix fem.* nicht unterscheiden; selbst an unserer deutschen Pflanze dieses weiblichen Farn habe ich noch weit grössere Abänderungen gefunden, die von einigen als verschiedene Arten betrachtet werden."

In 1810 Willdenow⁴ adopted Michaux's species, treating it as *Aspidium asplenoides*, and citing as synonyms both the *Nephrodium asplenoides* of Michaux and the *Asplenium Athyrium* of Sprengel. He says of it, "A sequenti [*A. Filix-femina*] praeter formam frondis parum diversum, soris lunatis abunde distinctum." He introduces a change into the description, saying, "pinnulis lineari-lanceolatis inciso-dentatis," a change which is certainly not in the direction of greater accuracy, and which seems to have lead to considerable confusion. Willdenow gives the habitat of "*Aspidium Filix femina*" as

¹ Michaux, Fl. Bor.-Am. ii. 268 (1803). The original description reads: [*Nephrodium*] ASPLENIODES. N. majusculum, glabrum: stipite nudo: fronde bipinnata; pinnulis subovaliblongis, inciso-dentatis; dentibus inferioribus obtusis, supremis mutice acutis: punctis utrinque juxta nervum lunatis.

Obs. Affine POLYP *Filici foem.* et forsan varietas. Puncta maturitatem quasi lineolae plerumque arcuatae; .ita ut proximitatem as ASPLENIUM indigent.

HAB. a Nova Anglia ad Carolinam.

This description and the range given apply distinctly to the more northern of our two eastern species. A fragment in the herbarium of the New York Botanical Garden, consisting of two pinnules labelled "from Herb. Michx. Poly. asplenoides a Nova Anglia ad Carolinam" confirms this application of Michaux's name.

² Sprengel, K., Anleit. zur Kent. der Gew. iii. 113 (1804).

³ Schkuhr, Ch., Kryptogamische Gewächse, 72 (1809).

⁴ Willdenow, C. L., Sp. Pl. v. 276 (1810).

"Europe," and describes a third species, *Aspidium angustum*, founding it upon the fern called by Michaux, "*Nephrodium Filix foemina*."¹

Almost immediately after Willdenow had thus cleared up the status of the American lady ferns, Pursh² introduced an element of confusion. He lists *Aspidium asplenoides* and *A. angustum*, quoting Willdenow's short diagnosis of each, and between them inserting *A. Filix-femina* with Willdenow's diagnosis of that species and the statement, "In low shady grounds: Canada to Virginia. July 24. v.v." He also says of *A. asplenoides*, "A tall species much resembling the following in many respects," and of *A. angustum*, "Resembling the following."

The history of the treatment of these ferns by American botanists during the next twenty-five years, was largely a series of attempts to fit the existing plants into the three species as outlined by Pursh. In these attempts reliance seems to have been placed almost entirely on the form and details of the fronds, while the real distinctions were ignored. It is accordingly often difficult to ascertain what species or form any particular author had in mind when he used a certain name. This confusion is especially evident if one compares, for example, the various editions of Amos Eaton's Manual of botany.³

¹ Willdenow, loc. cit. 277. The original description reads:

129. *ASPIDIUM angustum* W.

A. frondibus bipinnatis, pinnulis lanceolatis inciso-serratis, serraturis subbidentatis, infima superiore elongata, soris oblongis sublunatis. W.

Nephrodium (Filix femina) majusculum ***** *Mich. amer.* 2. p. 268.

Schmallaubiger Wurmfarn. W.

Habitat in Canada. 24. (v. s.)

Stipes glaber. Frons oblonga bipinnata pedalis et altior. Pinnae sesqui- seu bipollicares lanceolatae valde acuminatae alternae. Pinnulae trilineares suboppositae lanceolatae acutae inciso-serratae. Serraturae breves obtusiusculae indivisae vel bidentatae, infima superior reliquis longior. Sori oblongi parum lunati. A. praecedente [A. Filix-femina] satis distincta, circumscriptione frondis oblonga multo angustiore, pinnis magis acuminatis, serratura infima superiore pinnulae majore, soris non rectis sed leviter lunatis. W.

It is evident that Willdenow was describing a very small sun-form of our northern species. Specimens in the Gray Herbarium collected by C. G. Pringle in the province of Quebec in 1879 and 1880 correspond entirely to this description, nearly all others are larger.

² Pursh, F., *Flora Am.* Sept. 664 (1814).

³ It may be noted that a few American botanists refused to follow Pursh's lead. Thus Jacob Bigelow, in his *Florulae Bostonensis* (p. 254, 1814) lists only "*Aspidium asplenoides* Muhl." [sic], though his description, evidently drawn from actual material, indicated that he was dealing with one of the larger forms of *A. angustum*, and he persisted in this treatment of the ferns about Boston throughout the three editions of his work. The Pennsylvania botanists, Barton and Darlington (Barton, W. P. C., *Compendium Florae Philadelphiae*, ii. 209. 1818. Darlington, Wm., *Flora Cestrica* ed. 2, 579. 1837.) listed only a single species, *Aspidium asplenoides*. Darlington gives a good original description which indicates that he had named the species correctly. Unfortunately, in his third edition (1853) evidently under the influence of Hooker and Gray, he changed the name to *Asplenium Filix-foemina* R. Br.

The next stage in the treatment of the North American lady ferns, is that represented by the work of W. J. Hooker, Asa Gray and D. C. Eaton. Hooker at first ¹ reduced all the lady ferns of British North America, eastern and western, to *Athyrium Filix femina* with variety β (*Aspidium angustum* Willd.) and var. γ of the northwest coast. In both the typical species and his var. β he included western as well as eastern forms. He later ² transferred the species to *Asplenium*, and discarded all varieties. In his *Species Filicum* he says, "I do not find any of the N. American forms to differ essentially from the European."

American authors since Hooker's time have generally followed him pretty closely. Thus in the first four editions of Gray's *Manual* (1848–1863) we find beneath the description of "*A[splenium] Filix-foemina*," the following explanation: "(*Aspidium Filix-foemina* and *asplenoides* Swartz.) — A narrow form is *Aspid. angustum*, Willd. Moist woods, common. July." In the fifth edition (1869) the concluding sentence is changed to "moist woods, common and very variable. July. (Eu.)", while in the sixth edition (1890, Watson and Coulter), the synonymy disappears entirely, and the description is followed merely by the statement, "Moist woods; common, and presenting many variable forms. July. (Eu.)." The only change in the seventh edition (1908, Robinson and Fernald) is the substitution of the word "cosmop." for "Eu."

Likewise in the earlier editions of Wood's *Class Book*, under "*A[splenium] Filix-foemina* Bernh." are cited the synonyms, "*Aspidium Filix-foemina* and *asplenoides* [sic] Sw. *A. angustum* W.", but beginning in 1861, these names disappear even as synonyms. D. C. Eaton ³ reduces all North American lady ferns to "*Asplenium Filix-foemina*." He says, "The so-called varieties of this fern are almost innumerable, but all pass into one another by various gradations. The chief forms occurring in North America are the following." He then enumerates and describes vars. *exile*, *angustum*, *latifolium*, *commune* and *cyclosorum*. His chief illustration (pl. 76, no. 1) is drawn from a specimen of *Athyrium asplenoides*.

European botanists have generally kept the east American ferns as species distinct from *Athyrium Filix-femina*, the most notable excep-

¹ Hooker, W. J., *Flor. Bor.-Am.* ii. 262 (1840).

² Id. *Species Fil.* iii. 219 (1860).

³ Eaton, D. C., *Ferns of N. A.* ii. 225 (1880).

tions being Mettenius¹, who reduced them to varieties, and Hooker, who as noted above finally discarded them entirely. Milde, in some of his earlier publications² identifies "*Asplenium Michauxii*" (*Athyrium angustum*) with the European *A. Filix-femina*, but in his *Filices*, he does not include the names of the American ferns in the synonymy, of *A. Filix-femina*, and under the treatment of that species, he makes the following enlightening statement:

"The American plant, very similar in habit to the European, produces several forms which seem to be wanting in Europe. a) I have found smooth yellowish spores, in others ridged and blackish. b) Indusia sometimes fimbriate, sometimes furnished with cilia ending in large hyacinthine glands. Generally I have found stalked glands also intermixed with the sori. c) The blade beneath is either glabrous, or covered with long, cylindrical, obtuse, 1-2 celled hairs. Here belong: *Athyrium asplenioides* Fée and Presl (*Aspidium* Sw.—*Asplenium Athyrium* Sprengel) and *Athyrium Michauxii* Fée (*Asplenium* Spr.—*Aspidium angustum* Willd.—*Asplenium elatius* Link). The American plant is worthy of more accurate examination from various regions."³

SYNOPTICAL TREATMENT OF THE LADY FERNS OF EASTERN NORTH AMERICA.⁴

- A. Rhizome creeping, not densely covered with persistent bases of the fronds; scales of stipes very few, seldom persistent, rarely over 4 mm. long, their cells relatively broad and with pale walls; frond widest near the base; indusia ciliate, the cilia ending in glands; spores nigrescent, reticulate or wrinkled.

¹ Mettenius, G., Über einige Farngat. vi. *Asplenium*, 199 (1859).

² Milde, J., Die Gefäss. Crypt. in Schles. 575 (1858).

³ *Planta Americana habitu Europaeae simillima formes complures procreat, quae in Europa deesse videntur.* a) *Sporas flavas laeves, in aliis formas subnigras verrucosas inveni.* b) *Indusia nunc fimbriata, nunc ciliis in glandulas magnas hyacinthinas exeuntibus instructa. Glandulae stipitatas etiam soris immixtas interdum inveni.* c) *Lamina subtus aut glabra est, aut pilis longis cylindricis, obtusis, 1-2 cellularibus obsita est.* Huc pertinent: *Athyrium asplenioides Fée et Presl.* (— *Aspidium Sw.*— *Asplenium Athyrium Sprengel*) et *Athyrium Michauxii Fée* (*Asplenium Spr.*— *Aspidium angustum Willd.*— *Asplenium elatius Link*). *Planta Americana digna est, quae ex diversissimis regionibus accuratius examinetur.* Milde, J., *Filices Europae et Atlantidis*, 52 (1867).

⁴ The variety of *Athyrium alpestre* which occurs in a few alpine situations in the Gaspé peninsula, is treated fully with the lady ferns of western America. It is readily distinguished from any other eastern species of *Athyrium* by the exceedingly narrow segments of the frond, and by its small round sori, entirely without indusium.

ATHYRIUM ASPLENIOIDES (Michx.) Desv.

Nephrodium asplenoides Michx. Flor. Bor.-Am. ii. 268 (1803).

Asplenium Athyrium Spreng. Anleit. iii. 113 (1804).

Athyrium asplenoides Desv. Prod. 266 (1827), (Mem. Soc. Lin. Paris, vi.).

Icones: Schkuhr, Krypt. Gew. plate 78; Eaton, D. C., Ferns of N. A. ii. plate 76, fig. 1-3; Lowe, Ferns Br. and Ex. v. plate 37.

The following two forms of this species may be recognized:

B. Pinnules under 15 mm. long, oblong to oblong-linear, obtuse.

A. asplenoides f. *typicum*.¹

In the Gray Herbarium all specimens of lady ferns from south of the Potomac and Ohio Rivers, and the state of Missouri are of this species, and all except those noted below under the forma *subtripinnatum* are of this, the typical form. The following are specimens of *A. asplenoides* f. *typicum* from more northern states:

MASSACHUSETTS: Waltham, July 27, 1901, *W. P. Rich* (N. E.²); Quaker Leonard Road, Brockton, September 8, 1907, *A. A. Eaton*; Sandwich, July 28, 1909, *E. W. Sinnott* (N. E.).

RHODE ISLAND: Cranston, July 14, 1884, *J. F. Collins*; near Harbor Pond, Block Island, September 13, 1913, *Fernald, Hunnewell* and *Long* no. 8339; Foster, September 11, 1910, *G. S. and K. A. Torrey* (N. E.); near Swamp Hill Reservoir, Lincoln, August 8, 1885, *J. F. Collins* (N. E.).

CONNECTICUT: Bridgeport, July 7, 1889, *C. K. Averil* (N. E.); woods north of Cave Brook, Guilford, August 4, 1882, *Wm. R. Dudley* (N. E.); Danbury, July 19-20, 1912, *E. J. Winslow* (N. E.); without locality, *D. C. Eaton*.

NEW YORK: Bedford Park, New York City, August 14, 1900, *Percy Wilson*; Staten Island, July 28, 1905, *Philip Dowell* no. 3962.

PENNSYLVANIA: Lily Lake, Lucerne Co., July 29, 1899, *A. A. Heller*; swamp two miles south of Refton, in Eozoic, September 23, 1901, *A. A. Heller*.

MARYLAND: Hyattsville, September 12, 1899, *W. R. Maxon* no. 310; near Bush River, two miles north of station, September 11, 1902, *G. H. Shull* no. 369; Cumberland, *Howard Shriver*.

DISTRICT OF COLUMBIA: near Hamilton Hill, Washington, September 22, 1899, *W. R. Maxon* no. 339.

OHIO: without locality, *I. H. Lea*.

MISSOURI: Montevallo, October 17, 1915, *B. F. Bush* nos. 7897 and 7897A.; Campbell, September 6, 1910, *B. F. Bush* nos. 6199 and 6199A.

BB. Pinnules about 2 cm. long, triangular lanceolate, pinnatifid with oblong obtuse segments. *A. asplenoides* f. *subtripinnatum*.

¹ See Plate 123, figures 3-4 and 7-10.

² (N. E.), in the herbarium of the New England Botanical Club.

ATHYRIUM ASPLENIODES forma **subtripinnatum**, forma nov., frondibus maximis subtripinnatis, pinnulis deltoideo-lanceolatis ad 2 cm. longis, 8–10 mm. latis subacutis pinnatifidis, segmentis ordinis tertii oblongis obtusis ad apicem dentatis pinnulis parvulis formae typicae similibus.

A rare and unusually large form in which the segments of the third order, rather than the pinnules show the characteristic blunt oblong form (Plate 123, figs. 5 and 6).

Specimens in the Gray Herbarium:

MASSACHUSETTS: rich wet situations in half shade, Coon Hollow Brook, Milton, September 19, 1901, *F. G. Floyd* no. 89 b (N. E.); West Tisbury, July 26, 1916, *F. C. Seymour*.

WEST VIRGINIA: Glady, Randolph Co., September 21, 1904, *J. M. Greenman* no. 32.

VIRGINIA: altitude 3500 ft. near Luray, August 15, 1901, *E. S. and Mrs. Steele* no. 233; altitude 3600 ft. near Luray, August 27, 1901, *E. S. and Mrs. Steele* no. 48 (TYPE).

AA. Rhizome horizontal or somewhat oblique, completely concealed by the thick fleshy bases of the old fronds; scales of the stipes usually dark brown, their cells very narrow, and with thick usually dark walls; frond widest near the middle; indusia usually toothed or short ciliate, or rarely long ciliate, never glandular; spores yellow brown, smooth or sparingly papillate.

ATHYRIUM ANGUSTUM (Willd.) Presl.¹

Aspidium angustum Willd. Sp. Pl. ed. 4, v. 277 (1810).

Asplenium Michauxii Spreng. Syst. iv. 88 (1827).

Asplenium elatius Link, Fil. sp. 94 (1841).

Athyrium angustum Presl, Rel. Haenk. i. 39 (1825) as to combination only, excluding description and specimens cited.

Asplenium Filix femina var. *Michauxii* Mett. Über einige Farngat. vi. Asplen. 199 (1859).²

Athyrium asplenoides var. *angustum* Moore, Index Fil. 179 (1860).

Athyrium Filix-femina var. *Michauxii* Burnham, Am. Fern Journ. vii. 54 (1917).

An exceedingly polymorphic species, varying but slightly in the characters of rootstock, scales, sori, indusia and spores, but very widely, in the form of the frond. On the basis of differences in the frond, the following varieties and forms may be recognized, though in every case they pass by imperceptible gradations into one another:

C. Fronds dimorphic, the fertile coriaceous, contracted, sori at maturity confluent and covering the lower side of the fertile pinnules. Sun-forms, found only in regions of hot summers.

¹ See Plate 123, figures 11–18.

² The frequently cited reference of this combination to Mettenius, Fil. Hort. Lips., 1856 is not correct. Mettenius there described the variety, but gave it no name.

- D. Longest pinnae of the fertile frond 5–12 cm. long, pinnules 4–12 mm. long, simple, sori mainly asplenioid; pinnules of sterile fronds oblong obtuse, but slightly toothed or lobed. *A. angustum* f. *typicum*.¹

Willdenow described the pinnae as 1.5–2 inches long, the pinnules as 3 lines long. This is about the minimum size for a fruiting specimen. All sun-forms with simple pinnules may be considered as belonging to the typical form. These are the forms to which the varietal names *angustum* and *Michauxii* have commonly been given. As thus limited, the typical *A. angustum* ranges from Maine and southern Quebec to Massachusetts and Pennsylvania, being more common northwards. It does not occur in the region about the Gulf of St. Lawrence.

In the Gray Herbarium are the following specimens of this form:

QUEBEC: North Wakefield, July 4, 1911, *John Macoun*, Herb. Geol. Surv. Canada no. 83900; Rivière Ste. Marguerite, Lower Canada, August 14, 1879, *G. S. Pringle*; Lower Canada, August 3, 1880, *C. G. Pringle*.

MAINE: Hartford, August 29, 1907, *J. C. Parlin* no. 2271; very dry open woods, No. Berwick, August 31, 1894, *J. C. Parlin*.

NEW HAMPSHIRE: roadside in the sun, Randolph, July 30, 1896, *E. F. Williams*; North Conway, August 14, 1877, herb. of *W. C. Lane*; Kensington and Seabrook, many specimens collected by *A. A. Eaton*, including his numbers 90, 145, and 182; Hampton Falls, August 3, 1899, *A. A. Eaton*; Mt. Vernon, August 1891, *M. L. Stevens*.

VERMONT: without locality, 1855, herb. of *D. C. Eaton*; Dorset, 1915, *E. H. Terry* (N. E.).

MASSACHUSETTS: in sun, Salisbury, July 23, 1899, *A. A. Eaton*; in moist woods, Ipswich, *Wm. Oakes*; near Boston, *C. E.* and *W. Faxon*; Sharon, September, 1905, *S. F. Poole* no. 50.

NEW YORK: Gouverneur, August 1900, herb. of *E. C. Anthony*.

PENNSYLVANIA: Bald Eagle Valley, Blair Co., 1860, *H. V. Bocking*; Friendsville, September 1, 1906, *M. H. Grant*; Pocono Plateau, 1904, *J. W. Harshberger*.

ONTARIO: Port Colborne, July 12, 1901, *John Macoun*, herb. Geol. Surv. Canada, no. 66416.

- DD. Longest pinnae of fertile frond 1–2 dm. long, pinnules 12–25 mm. long, pinnatifid, sori several on each of the lower segments, often horse-shoe shaped; pinnules of sterile fronds oblong lanceolate, strongly toothed or pinnatifid, somewhat acute.

A. angustum var. *elatus*.

ATHYRIUM ANGUSTUM var. **elatus** (Link), new comb.

Asplenium elatus Link, Fil. Sp. 94 (1841).

Link describes the frond of his fern as sub-tripinnatifid, 3 feet long, pinnae 4–6 inches long, scarcely 1 line wide. The larger sub-forms

¹ See Plate 123, figures 11 and 12.

with a tendency to have compound pinnules may be placed here. This variety is not found quite so far north as the typical form, and is more abundant southward. In situations where both this and the typical forms occur, it is quite possible that this form may represent merely a more mature state of the plant than the typical form (Plate 123, figs. 14-16).

A. angustum var. *elatus* occurs from Maine to Minnesota, south to Rhode Island, New York and Missouri.

The following are the specimens of this variety in the Gray Herbarium:

MAINE: North Berwick, July 27, 1894, *J. C. Parlin*.

NEW HAMPSHIRE: Kensington, August 3, 1899, *A. A. Eaton* no. 149; Nottingham, September 15, 1899, *A. A. Eaton* no. 303.

VERMONT: open roadside, Repton, July 7, 1908, *E. F. Williams*.

MASSACHUSETTS: in moist woods, Ipswich, *Wm. Oakes*; roadside, in sun, Rockport, August 15, 1897, *E. F. Williams*; in shady woods, Hyde Park, August 24, 1902, *F. G. Floyd* no. 1119A; open woods, Rowley, August 9, 1899, *E. F. Williams*.

RHODE ISLAND: dry open soil between Pilot Hill and Southeast Point, Block Island, August 20, 1913, *Fernald, Hunnewell and Long*, no. 8337.

CONNECTICUT: trap soil, Bluff Mountain, No. Guilford, August 19, 1906, *G. H. Bartlett*.

NEW YORK: Lake Mahopac, August 1848, herb. *J. Carey*; Lawrence, September 23, 1914, *Orra P. Phelps* no. 14; moist woods, Clayville, August 5, 1899, *B. D. Gilbert*; Castle swamp, Oneida, August 12, 1906, *H. D. House* no. 2763, September 22, 1907, *Nellie Mirick*; Elmyra, September 22, 1907, *E. J. Winslow*.

MICHIGAN: damp sandy ground, Rush Lake, Huron Co., August 22, 1907, *C. K. Dodge* no. 2; Lansing, July 7, 1887, *D. A. Pelton*; Wallace, Menominee Co., August 22, 1884, *J. H. Schuette*.

MINNESOTA: springy mud, St. Anthony (part of Minneapolis), July 20, 1888, *J. H. Schuette*.

MISSOURI: shaded banks, Dumas, *B. F. Bush* no. 5889.

CC. Fronds not dimorphic, coriaceous nor contracted, sori discrete at maturity. Forms of regions with cool summers, found also in dense shade in warmer regions.

E. Pinnules diminishing in size regularly toward the tip of the pinna, oblong or linear-lanceolate, 3-5 times as long as wide, regularly and coarsely toothed or pinnatifid, the basal anterior segment usually largest, the others regularly diminishing in size toward the tip of the pinnule.

F. Pinnules standing at a wide angle to the rachis of the pinna, often connected by a membranous wing along the rachis of the pinna, teeth or segments of pinnules obtuse.

G. Pinnules lanceolate, subacute, strongly toothed or pinnatifid, the segments toothed, membranous wing along the rachis obscure or wanting....*A. angustum* var. *rubellum*.

ATHYRIUM ANGUSTUM var. **rubellum** (Gilbert), new comb.¹

Athyrium filix-foemina rubellum Gilbert, List of N. A. Pterid. 35 (1901).

In the southern part of its range this variety appears to be merely the shade-form corresponding to the sun-forms discussed above, especially to the var. *elatus*, and its fronds are scarcely to be distinguished from the sterile fronds of that variety. The variety *rubellum*, however, ranges much farther to the north and east than either forma *typicum* or var. *elatus*, which appear never to occur in regions of cool summers.

The variety *rubellum* occurs throughout the range of the species, of which it appears to be the fundamental biological type, from which all the other varieties and forms have been derived. As here defined, it is not limited to forms with red stems, and hence it is unfortunate that we are obliged to adopt Gilbert's name. This is necessary, as authentic material of Gilbert's variety, collected by Gilbert himself, from his type locality, unquestionably belongs to the variety as here defined.

The following are the specimens of this variety in the Gray Herbarium:

NEWFOUNDLAND: barrens at the base of the serpentine tablelands, region of Bonne Bay; August 27, 1910, *Fernald* and *Wiegand* no. 2319; rocky border of hillside brook, Snook's Arm, Notre Dame Bay, August 19, 1911, *Fernald* and *Wiegand* no. 4284; Blow-me-down Mts., 1300 ft. altitude, August 4, 1908, *Eames* and *Godfrey* no. 5763; woods, Bay of Islands, August 9 and 10, 1901, *Howe* and *Lang* no. 1179; dry thicket, Bay St. George, August 5-7, 1901, *Howe* and *Lang* no. 989.

QUEBEC: low wet margin of Seal Cove River, Douglastown, Gaspé Co., August 22, 1904, *Collins*, *Fernald* and *Pease*; Bic, Rimouski Co., July 15, 1907, *Fernald* and *Collins* no. 817; Cap à l'Aigle, July 13, 1905, *John Macoun*, herb. Geol. Surv. Canada no. 69251; Little Metis, August 21, 1906, *James Fowler*.

PRINCE EDWARD ISLAND: roadsides thickets and borders of dry woods, August 29, 1912, *Fernald*, *Long* and *St. John* no. 6664.

NEW BRUNSWICK: in partial shade along a fence, Shediac Cape, August 2, 1914, *F. T. Hubbard*.

NOVA SCOTIA: Baxter's Harbor, July 10, 1900, *F. G. Floyd* no. 680; rich soil, edge of woods, Pictou, July 12-18, 1901, *Howe* and *Lang* no. 547; dry woods, Pictou, July 12-18, 1901, *Howe* and *Lang* no. 546; rich moist bank, Yarmouth, June 22-29, 1901, *Howe* and *Lang* no. 111; Kentville, July 11, 1900, *F. G. Floyd* no. 686.

MAINE: rich woods, Canton, August 1, 1908, *J. C. Parlin*.

NEW HAMPSHIRE: woods, Randolph, July 7, 1894, *E. F. Williams*. Alton Bay, *A. A. Eaton*; low woods, Jaffrey, July 21, 1897, *B. L.*

¹ See Plate 123, figure 13.

Robinson no. 249; roadside, Kingston, August 3, 1899, *A. A. Eaton* no. 150; East Kingston, June 24, 1900, *A. A. Eaton*; Hampton Falls, August 5, 1899, *A. A. Eaton*.

VERMONT: woods, Hancock, July 5, 1905, *E. F. Williams*; Manchester, July 21, 1898, *M. A. Day* no. 233.

MASSACHUSETTS: great swamp, Amesbury, June 24, 1899, *A. A. Eaton* no. 49; Boston, *C. E. Faxon*; id. *W. Faxon*; rich shady woods, West Roxbury, July 13, 1902, *F. G. Floyd* no. 1044; wet rich shady woods, Hyde Park, July 6, 1902; *F. G. Floyd* no. 1032A; shady woods, Milton, July 5, 1902, *F. G. Floyd* no. 1028; sandy bank, Concord, August 10, 1908, *E. F. Williams*.

CONNECTICUT: low woods, Southington, July 18, 1899, *C. H. Bissell*.

NEW YORK: Trout Lake, Hermon, September 4, 1900 (two collections), *B. D. Gilbert*; Clayville, July 25, 1899, *B. D. Gilbert* (type material of *Gilbert's A. filix-foemina rubellum*); bottom woods, Gouverneur, July 1900, *E. C. Anthony*; river bank, Pine Grove, July 8, 1894, *Grace Gilbert*.

PENNSYLVANIA: Friendsville, September 1, 1906, *M. H. Grant*.

ONTARIO: Ottawa, August 21, 1915, *Fr. Rolland* no. 135; Plevna, August 11, 1902, *J. Fowler*.

OHIO: Newark, May 6, 1905, *H. A. Gleason*.

MICHIGAN: moist woods, Hamlin Lake, Ludington, Mason Co., July 7, 1910, *Ralph W. Chaney* no. 109; among rocks in low places, Keweenaw Co., August, 1889, *O. A. F[arwell]*.

ILLINOIS: Lincoln, July 4, 1899, herb. of *H. A. Gleason* no. 778.

WISCONSIN: Milwaukee, *I. A. Lapham*.

MINNESOTA: White Bear Lake, July 17, 1885, *J. H. Schuette*.

MISSOURI: Canton, May 30, 1906, *John Davis*; rich woods, Sibley, June 30, 1906, *B. F. Bush* no. 3999.

SOUTH DAKOTA: Sylvan Lake, Black Hills, altitude 6000–6500 ft., July 20, 1892, *P. A. Rydberg* no. 1195.

GG. Pinnae acute, pinnatifid pinnules oblong, obtuse, obscurely toothed, membranous wing along the rachis of the pinna strongly developed.

A. angustum var. *laurentianum*.

ATHYRIUM ANGUSTUM var. **laurentianum**, var. nov., frondibus ac fertilibus ac sterilibus consimilibus membranosis, pinnis pinnatifidis acutis, pinnulis oblongis obscure serratis ala membranosa conjunctis, soris haud confluentibus ex pinnae costa remotis.

A northeastern variety with fronds corresponding to those of young plants of the variety *rubellum*, but the ample fruiting, and the strongly developed rootstock indicate clearly that the plants are mature. The range of this plant is indicated by the following list of the specimens in the Gray Herbarium:

LABRADOR: Wabek Harbor, August 4, 1891, *Bowdoin College expedition to Labrador* no. 215.

NEWFOUNDLAND: boggy places on hill southwest of Tilt Cove,

Notre Dame Bay, August 22, 1911, *Fernald* and *Wiegand* no. 4285; rich shaded soil, Torbay, August 21–26, 1901, *Howe* and *Lang* no. 1433; woods, Virginia Water, August 5, 1894, *Robinson* and *Schrenk*; low damp clearings, Grand Falls, valley of Exploits River, July 20, 1911, *Fernald* and *Wiegand* no. 4283; Mc. Weils Cove, Bay of Islands, August 24, 1896, *A. C. Waghorne* no. 29; Birchy Cove, Bay of Islands, August 24, 1896, *A. C. Waghorne* no. 24; damp thickets, Bay St. George, August 5–7, 1901, *Howe* and *Lang* no. 1006a.

QUEBEC: eastern granite slopes, Table-Topped Mt., Gaspé Co., August 9 and 11, 1908, *Fernald* and *Collins* no. 275 (type); alpine bogs, Mt. Albert, Gaspé Co., July 21–23, 1906, *Fernald* and *Collins* no. 273.

MAINE: moist woods, Princeton, Washington Co., August 3, 1912, *S. N. F. Sanford* (N. E.).

EE. Adjacent pinnules varying irregularly from one another, irregularly lobed and toothed.

H. Pinnules 5–8 mm. broad, 10–18 mm. long, joined by a broad membranous wing, lobes of the pinnules broad and overlapping.....*A. angustum* forma *confertum*.

ATHYRIUM ANGUSTUM forma **confertum**, forma nov., foliis ac fertilibus ac sterilibus consimilibus, pinnis pinnulisque imparibus, pinnis basin versus pinnatis, apicem versus pinnatifidis, pinnulis confertis ad 8 mm. latis, segmentis ordinis tertii imparibus confertis.

A form of *A. angustum* corresponding in the irregular cutting and overlapping of the broad pinnules to *A. Filix-femina* var. *latifolium* Babington, but with all the technical characters of *A. angustum*. Apparently this is a somewhat abnormal form without geographical significance as appears from the following list of specimens:

QUEBEC: boggy subalpine woods, altitude 1000 m., Table-topped Mt., Gaspé Co., August 13, 1906, *Fernald* and *Collins* no. 276 (type).

NEW HAMPSHIRE: Hampton Falls, August 5, 1899, *A. A. Eaton*.

MASSACHUSETTS: Brockton, September 8, 1907, *A. A. Eaton*.

The New England specimens are not so far removed from the ordinary var. *rubellum* as is the Gaspé specimen.

HH. Pinnules very irregular in size and shape, with many long acute teeth which project in various directions.

A. angustum forma *laciniatum*.

ATHYRIUM ANGUSTUM forma **laciniatum**, forma nov., frondibus ac sterilibus ac fertilibus consimilibus pinnulis erosis dentibus spinulosis incompositis instructis.

An abnormal form of fairly frequent occurrence, in which the frond looks as if it had been nibbled when young, some of the pinnules being wanting or greatly reduced, and all of them tending to show great irregularity of form. The teeth of the margins of the pinnules are unusually long and acute, and are inclined to stand out in a very irregular and disorderly fashion.

It corresponds exactly to the similarly named "variety" of *A. Filix-femina*. The following is a list of the specimens of this form in the Gray Herbarium:

MAINE: rocky bank of woodland stream, Buckfield, July 23, 1908, *J. C. Parlin* no. 2617.

VERMONT: in sun, edge of woods, Windham, August 30, 1902, *W. H. Blanchard* (type); Westmore, August 6, 1908, *E. J. Winslow* no. 21 (varying but slightly from the normal).

MASSACHUSETTS: low rich woods, West Roxbury, August 2, 1902, *F. G. Floyd* no. 1075.

NEW YORK: under tree in garden, Gouveneur, July 1900, *E. C. Anthony*.

FF. Pinnules oblique to the rachis of the pinna and prominently decurrent, though usually not connected by a membranous wing, teeth of pinnules acute... *A. angustum* forma *elegans*.

ATHYRIUM ANGUSTUM forma **elegans** (Gilbert), new comb.

Athyrium filix-foemina elegans Gilbert, List of N. A. Pterid. 33 (1901).

A somewhat rare form with markedly oblique and decurrent widely spaced pinnules, the basal anterior pinnule usually much larger than the others. The following specimens in the Gray Herbarium are definitely of this form:

MAINE: Bar Harbor, herb. of *Francis H. Peabody*.

NEW HAMPSHIRE: Nottingham, July 17, 1900, *A. A. Eaton* no. 422.

RHODE ISLAND: Cranston, July 14, 1884, *J. F. Collins*.

NEW YORK: Trout Lake, Herman, September 4, 1900, herb. of *E. C. Anthony*.

ONTARIO: Owen Sound, *Mrs. Roy* (an exceedingly large specimen, nearly thrice pinnate, but showing the general character of this form).

It is notable that certain ferns of eastern Asia seem to be identical with certain of the American forms of *A. angustum*, having small dark scales similar in structure to those of the American plant, fronds moderately reduced downward, and sori with the characteristics of *A. angustum*. None of these specimens shows any part of the rhizome, so that it is impossible to say definitely whether *A. angustum* really reappears in eastern Asia like so many other east American plants, or whether it has there merely a representative species of very close affinity.

The specimens in question are: Northern China, 1910, *Wm. Purdom* no. 48, apparently *A. angustum* var. *typicum*; ad. fl. Schilka, Dahuria, *Turczaninow*, labelled "*Asplenium Filix Feomina* Bernh. var. *tripinatum* Rupr.," evidently some of the material referred by Ruprecht

himself to that variety with the comment “forma rigida”¹; Manchuria, ad. fl. Amur, 1855, *R. Maack*; the last two specimens appear to be var. *rubellum*; North China, 1886, *H. E. M. James* no. 192, close to var. *elatius*.

If these ferns should prove to be conspecific with the similar North American forms, an interesting nomenclatorial question would be raised concerning the status of Ruprecht's varietal name *tripinnatum*.

4. THE LADY FERNS OF ALASKA, WESTERN CANADA AND THE NORTHWESTERN STATES.

In 1901, Gilbert recognized clearly the points of difference between the lady ferns of the northwestern states, British Columbia and Alaska and those of the eastern states.² So traditional, however, had become the view that our eastern ferns were true *Athyrium Filix-femina*, that Gilbert seems never to have noticed that, in the various points of difference which he noted, it is always the western, rather than the eastern plant which approaches most closely to the European type. Thus he says of the western fern, which he called *Athyrium cyclosorum* Ruprecht, “Indusium short, fringed early in the season with long, jointed cilia which disappear with age, generally hippocrepiform, sometimes only hamate,” and a little lower on the page he mentions the “rotund sorus and jointed cilia of the indusium,” descriptions which correspond perfectly with much of the European material. In a later publication³ he mentions a color peculiarity (by no means general in western lady ferns) and then goes on to say, “the shape of the frond is very much like that of *Struthiopteris*. It tapers from the middle both ways, and the small lower pinnae come within four inches of the root. The farther down the stipe the pinnae are situated, the farther apart they stand. The pinnae themselves are quite different from those of *Asplenium filix-foemina*. Not only are they cut differently, but the enlargement of the anterior lower lobe, which is so distinct a feature of *A. f. f.* is entirely lacking here.” It will be remembered that one of the diagnostic characters by which Willdenow distinguished his *Aspidium angustum* from the true *Filix-femina*, was

¹ Ruprecht, F. J., Dist. Crypt. Vasc. in Imp. Ros. 41 (1845).

² Gilbert, B. D., Working List of N. A. Pterid. 31 (1901).

³ Id. Obs. on N. A. Pterid. Fern Bull. xiii. 76 (1905).

that the *former* species has "serraturis subbidentibus, infima superiore elongata."

A comparison of the specimens in the Gray Herbarium of *Athyrium Filix-femina* from western North America, with those from Europe shows that in all important respects there is complete agreement. Rhizome, scales, general form of frond, sori, indusia, sporangia and spores all agree. The indusia of the larger sori, measured in over twenty-five specimens give an average height of 0.55 mm., and an average length of 0.8 mm., precisely the dimensions obtained from European material.

The stalks of the sporangia proliferate as they commonly do in European material of *A. Filix-femina*. No case has been seen in west American material in which a branch of the sporangial stalk bears a glandular structure such as is common in the east American species, and is occasionally found in European material of *A. Filix-femina*.

The spores are yellowish, and average $38.9 \times 24 \mu$ in size.

Like the European *A. Filix-femina*, the northwestern plant is very variable. Some forms are common to both continents, while others appear to be peculiar to one or the other. The coarser European forms may be matched exactly with American material, while some of the finer cut forms, particularly var. *multidentatum* (Döll) Milde, and the form commonly known in Europe as var. *rhaeticum*,¹ appear to be wanting in this continent. A characteristically American variety is *A. Filix-femina* var. *sitchense* Ruprecht ex Moore,² a large and coarse

¹ This is the *Polypodium rhaeticum* of Linnaeus in part. As explained below on page 203 the Linnaean name is a nomen confusum, and should be rejected. The oldest tenable varietal name for this plant appears to be *Athyrium Filix-femina* var. *convexum* Newman, Hist. of Brit. Ferns, ed. 2, 245 (1844).

² Moore, Thomas, Index Fil. 183 (1860), where this combination appears in the synonymy, and is attributed to Ruprecht. Ruprecht's own publication in Dist. Crypt. Vasc. Imp. Ross., 41 (1845), was as follows:

65. *Athyrium Filix foemina* Roth, * * * * *

65β. *Athyrium Filix foemina*: tripinnatum * * *

65γ. *Athyrium cyclosorum* * Indusium brevius et sori plerumque rotundi. Petropawlowsk! (etiam pinnulis angustis) et Unalaschka!; Kadiak (Blaschke!). Ut videtur etiam pr. Kola in Lappon. ross. crescit. (Hb. Baer!).

65δ. *Athyrium sitchense* * Frons interdum 4 pedalis; indusia brevissima fere cystopteridis; pinnae primariae secundariae pl. min. spatio pollicis dimidii disjunctae. Sitcha (Mertens!).

This publication of "*γ Athyrium cyclosorum*" and "*δ Athyrium sitchense*", has been cited by various authors, sometimes as the publication of species, and sometimes as that of varieties. Ruprecht, himself, in the preface to his paper (loc. cit., p. 6) speaks of them as "species secundi ordinis s. d. varietates characteres suos interdum constanter servantes."

Ruprecht's other subspecies, *γ Athyrium cyclosorum*, has been identified with the var. *sitchense* by many authors, and the name has been applied to some or all of our western lady ferns. As

variety sometimes 2 m. tall, pinnae 1–2 dm. long, remote, the lower ones with 5–10 cm. intervals; pinnules triangular-lanceolate, 1.5–3 cm. long, 0.5–1.5 cm. wide, remote, separated by about their own width, incised with numerous low, broad and blunt teeth, or in the largest fronds, pinnatifid, the segments of the third order oblong, obtuse, slightly 5–8 toothed, the largest 6×2.5 mm. in size.

This variety differs from *A. Filix-femina* var. *multidentatum* (Döll) Milde of Europe, chiefly in its relatively broad and short ultimate segments with almost suppressed marginal teeth, which are crowded towards the very obtuse apex of the segment. The immature form of this variety is the forma *Hillii*.² The pinnules at this stage are large ($4-5 \times 7-10$ mm.), very blunt and rounded, crowded, and not at all pinnatifid, but with a somewhat crenate outline and numerous very small teeth borne chiefly at the summit of the pinnule. This type of foliage is retained until after fruiting commences, and until the fronds are 5–6 dm. tall. The transition to the mature form may sometimes

has already been pointed out, there is nothing about the sori of the American ferns of this species to distinguish them from many Scandinavian, German, and British specimens. Accordingly, Ruprecht's definition of γ *A. cyclosum* becomes nearly meaningless, and his reference to Lapland in his statement of habitat indicates that he was including in his variety all those lady ferns which have unusually short and round sori. Some of his Alaskan material assigned to this variety is here considered as belonging to the var. *sitchense*, while the Asiatic (probably) and the European (certainly) is considered as typical *A. Filix-femina*. In this interpretation I am following Milde, who says (Fil. Eu. et At. p. 50, 1867.) "var. *cyclosum* Rupr. ex insulis Kadjak et Unalaschka mihi nomine varietatis non digna videtur; specimina unalaschkensia paulum varietatis praecedentis [var. *sitchense*] nos commonent, and again, on p. 52 of the same work, "*Athyrium cyclosum* Rupr. Beitr. III (1845) p. 41 nullo modo ab *A. Fil. fem.* differt."

Gilbert (List of N. A. Pterid. 31) says, "The only [specimens] in the U. S. which can be considered as something like type specimens are two in the Gray herbarium which were received from St. Petersburg: one of them came from the Amur region, the other from Unalaska which was the type locality." The first mentioned specimen cannot be identified, as there are in the Gray Herbarium three specimens of lady ferns from the Amur region, all received by way of Petrograd, and all labelled "*Aspidium Filix foemina*." None of these shows any especial resemblance to the west American forms of this species. The Unalaska specimen is labelled, apparently in Ruprecht's own hand-writing, "*Aspidium Filix foemina* var. *aspidioides* Ruprecht," and has the printed data "Herb. Acad. Petrop.—Unalaschka.—Dr. Mertens." While this is probably some of the original material from which Ruprecht published his γ *A. cyclosum*, it cannot be considered as type material, considering that it does not bear that name, nor any recognized synonym. It is a fairly well marked example of the var. *sitchense* as here defined. A specimen labelled in the same hand-writing, "*Athyrium Filix foemina* (L.) Roth. var.—Kamtschatka" is typical *A. Filix-femina*.

The synonymy of the var. *sitchense* is, therefore:

ATHYRIUM FILIX-FEMINA (L.) Roth. var. SITCHENSE Ruprecht ex Moore, Index Fil. 183 (1860).

δ *Athyrium sitchense* Rupr. Dist. Crypt. Vas. Ross., 41 (1845).

γ *Athyrium cyclosum* Rupr. loc. cit. 41 (1845), in part.

² ATHYRIUM FILIX-FEMINA (L.) Roth. var. SITCHENSE Ruprecht ex Moore forma **Hillii** (Gilbert) comb. nov., *Athyrium cyclosum* f. *Hillii* Gilbert, List of N. A. Pterid, 32 (1901).

be seen in a single frond, the lower pinnae showing the immature form, and the upper ones, the mature. As the immature type of foliage appears to be sub-permanent in some cases, it seems to be worthy of a formal name.

An extreme sun-form of the var. *sitchense* is the forma *strictum*,¹ which has narrowly lanceolate pinnules with revolute margins. It closely resembles the European var. *convexum* Newman, but may be distinguished from that variety by the lower pinnae, which in the European form are modified like the upper ones, whereas in the form now under consideration they are but slightly contracted, and resemble the basal pinnae of the typical var. *sitchense*.

Athyrium Filix-femina var. *sitchense* occurs from the Aleutian Islands to California,² chiefly near the coast, also at low altitudes in the Selkirk Mountains of British Columbia, and in northern Idaho.

American specimens of typical *Athyrium Filix-femina* in the Gray Herbarium:

IDAHO: near Lakeview, Kootenai Co., August 1-10, 1892, A. A. Heller; in damp forest at Mullan, Coeur d'Alene Mts., altitude 3000 ft., August 7, 1895, J. B. Leiberger no. 1493.

OREGON: Calapooga, Douglass Co., 800 ft. altitude, July 26, 1899, M. A. Barber, no. 125.

WASHINGTON: Stevens Pass, Cascade Mts. August 17, 1893, Sandberg and Leiberger, no. 771; deep canyon near springs, Blue Mts., Columbia Co., August 7, 1897, R. M. Horner no. B. 598; Tacoma, Sept. 17, 1898, J. B. Flett; Clark Springs, Spokane, June 26, 1902, F. O. Kreager, no. 34; without locality, G. R. Vasey, no. 45.

BRITISH COLUMBIA: Selkirk region: Upper Spillimacheen, altitude 6500 ft., August 3, 1904, C. H. Shaw no. 438; Spillimacheen valley, altitude 6000 ft., July 30, 1904, L. R. Heacock, in Shaw's Selkirk Flora, no. 421; near mouth of Downie Creek, altitude 1900 ft., August 9, 1905, C. H. Shaw no. 1127; Rogers Pass, altitude 4400 ft., August 9, 1904, E. R. Heacock, in Shaw's Selkirk Flora, no. 444; Goldstream, altitude 2200 ft., August 3, 1905, C. H. Shaw no. 1069.

Coast region: New Westminster, June 1899, A. J. Hill; on rocks in shady places, Pt. Renfrew, Vancouver Island, June-July 1901, Rosendahl and Brand, no. 106.

Specimens of *Athyrium Filix-femina* var. *sitchense* in the Gray Herbarium:

IDAHO: along creeks near Rathdrum, Kootenay Co., July 25, 1892, McDougal and Heller, no. 723.

¹ *ATHYRIUM FILIX-FEMINA* (L.) Roth var. *SITCHENSE* Ruprecht ex Moore forma **strictum** (Gilbert), comb. nov., *Athyrium cyclosorum strictum* Gilbert, loc. cit., 32 (1901).

² I have seen a single specimen of this variety from California. It is in the collection of Mr. R. A. Ware of Boston, and was collected by R. J. Smith near Sur River, Monterey Co. It was distributed as *Dryopteris spinulosa dilatata*.

OREGON: without locality, *Elihu Hall* no. 682 (f. *Hillii*).

WASHINGTON: Columbia River, 1841, *Hinds*; without locality, *G. R. Vasey* no. 47 (f. *strictum*), and no. 46; Ewell's yard, Quinault, June 25, 1902, *H. S. Conard* no. 154; Cheney, *Mrs. Susan Tucker*.

BRITISH COLUMBIA: Selkirk region: Revelstoke, altitude 1600 ft. July 22, 1890, *John Macoun* (f. *strictum*), and July 3, 1905, *C. H. Shaw* no. 793; Glacier, altitude 3900 ft., August 8, 1909, *Butters* and *Holway* no. 475.

Coast region: New Westminster, 1899, *A. J. Hill*, an extensive series of specimens illustrating different stages in the development of this fern, and including type material of Gilbert's two forms.

ALASKA: "Unalaschka, Dr. Mertens," from Herb. Acad. Petrop., labelled in Ruprecht's writing, "*Athyrium Filix foemina* var. *aspidioides* Ruprecht"; White Pass, July 23, 1914, *Alice Eastwood* no. 874; Skagway, July 20, 1914, *Alice Eastwood* no. 796.

4. THE LADY FERN OF CALIFORNIA,¹ THE BASIN REGION, AND THE SOUTHERN ROCKY MOUNTAINS.

The lady fern of this region has been treated by all American authors as the true *Athyrium Filix-femina*. It is, however, found to differ from the typical form of that species in several minor respects, and in one important character. It should, therefore, be considered as a well marked geographical variety:

ATHYRIUM FILIX-FEMINA (L.) Roth. var. **californicum** var. nov.
differt a forma typica paleis atris, indusiis interdum dentatis
vel brevissime ciliatis, sporis majoribus reticulatis nigrescentibus.

The scales of this variety are usually considerably darker than in typical *A. Filix-femina*, but as in the case of similar dark scales found occasionally in European specimens, they have the same structure as the ordinary pale scales of *A. Filix-femina*, and not the fibrous structure characteristic of the dark scales of *A. angustum*. Short asplenoid sori are more frequent than in typical *A. Filix-femina*, and the indusia are seldom long ciliate, but rather short ciliate or merely toothed. In this respect they resemble those of *A. angustum*, but their dimensions are rather those of typical *A. Filix-femina*. They measure, on the average, 0.5 mm. high, and 0.8 mm. long. As in all American forms of *A. Filix-femina*, the sporangia are entirely without stalked glands. The most important peculiarity of this variety is the character of the spores, which are unusually large, averaging $43 \times 27.5 \mu$,

and which have a distinct nigrescent, wrinkled and reticulate exospore similar to that found in *A. alpestre* and in *A. asplenoides*.

In its underground parts, and in the form of the frond, this variety is in no way peculiar. The frond is rather variable but generally agrees closely with ordinary European forms. It is usually markedly puberulent on the rachis and the back of the pinnae.

It ranges from California eastward to southern Idaho, Colorado and New Mexico. It also extends southward into Mexico, at least as far as the state of Chihuahua.

All specimens of *A. Filix-femina* in the Gray Herbarium within this range belong to this variety except that in Idaho and Wyoming some specimens occur which are intermediate between this variety and typical *A. Filix-femina*. These transitional forms have intermediate types of spores, or spores which are variable in type even on the same frond.

The following list contains a portion of the material of this variety in the Gray Herbarium:

COLORADO: Tabeguache Basin, 8000 ft., August 20, 1913, *Edwin Payson* no. 195; Fish Creek Falls, Routt Co., July 21, 1903, *Leslie N. Goodding* no. 125.

IDAHO: Trinity, Elmore Co., August 23, 1910, *J. F. Macbride* no. 635, distributed as *Cystopteris languida* A. Nels. n. sp.

UTAH: City Creek Canyon, August 9, 1884, *F. E. Leonard*, ex herb. Oberlin College, no. 201.

NEW MEXICO: Mogollon Mts., 7500 ft., Socorro Co., July 23, 1903, *O. B. Metcalfe* no. 298.

NEVADA: Little Valley, Washoe Co., 2000–2155 M., August 14, 1902, *C. F. Baker* no. 1466; Snow Valley, Ormsby Co., August 8, 1902, *C. F. Baker* no. 1444.

CALIFORNIA: Dollar Lake Canyon, San Geronio Mts., altitude 9000–9500 ft., July 12, 1908, *Abrams* and *McGregor*, no. 768, Mt. Eddy, Siskiyou Co., August 26, 1915, *A. A. Heller* no. 12234; Mt. Rose, near Webber Lake, August 15, 1874, *J. G. Lemmon*; outlet of Lake Chequita, Madera Co., August 16, 1895, *J. W. Congdon* no. 79 (TYPE).

Specimen: intermediate between *A. Filix-femina* and *A. Filix-femina* var. *californicum*:

WYOMING: Piney Creek, Bighorn Mts., August 28, 1900, *J. B. Jack*.

5. *ATHYRIUM ALPESTRE* AND ITS AMERICAN VARIETY.

The typical form of *Athyrium alpestre* (Hoppe) Rylands ex Moore¹ is an arctic-alpine plant of Europe, ranging from Iceland to Asia Minor. In habit and foliage it greatly resembles *A. Filix-femina*, from which it differs in its spores, which are nigrescent and reticulate, and in its sori, which are smaller than those of *A. Filix-femina*, almost perfectly round, and seemingly without any indusium. Careful dissection shows, however, that the receptacle of the sorus is slightly elongated along the vein, and under a compound microscope it is almost always possible to find a vestigial indusium in the same position that the indusium holds in forms of *A. Filix-femina* with round sori. This indusium is about 0.3 mm. high, and may extend along the vein for as much as 0.25 mm., but often consists merely of two or three hairs joined together side by side at the base. Its cilia are always swollen and glandular at the tip.

The peculiarly reduced condition of the sorus and indusium in this species has often lead to its being placed in genera far removed from the group now under consideration. Its structural general resemblance to *A. Filix-femina* is, however, very great, and the latter species occasionally has semi-abortive sori with indusia almost as reduced as those of *A. alpestre*.

A common arctic-alpine plant of North America has been traditionally identified with this species, but it differs in having the ultimate segments of the frond conspicuously narrower, and more widely separated from one another, and the sori even smaller than in the type (0.5–0.7 mm. in diameter as against 0.75–1.0 mm. in the typical form), sub-marginal and protected by a reflexed tooth of the pinnule. Care-

¹ *ATHYRIUM ALPESTRE* (Hoppe) Rylands ex Moore.

Aspidium alpestre Hoppe, Neue Taschenbuch 216 (1805).

Phegopteris alpestris Mett. Fil. Hort. Lips. 83 (1856).

Athyrium alpestre Rylands according to Moore, Ferns of Gr. Br. and Ir. Nat. Print. Fol. ed. Pl. 7 (1857).

Polypodium rhaeticum L. Sp. Pl. ii. 1091 (1753), in part.

Polypodium Rhaeticum L. was made up of a mixture of this plant and certain forms of *A. Filix-femina* which resemble it in the form of the frond. The latter alone are represented in the Linnaean herbarium under this name, while to the former belongs probably the name-bringing synonym, Bauhin's *Filix rhaetica tenuissime dentata*. With sundry variations the Linnaean name has been employed extensively for both of these ferns. This seems to be a clear case of a nomen confusum, which should be rejected under the international rules. For a further discussion of this question, see P. Ascherson, Oesterreicher Bot. Zeit. 46: 44. 1896.

ful search has failed to disclose any vestige of indusium in the American material.

As certain intermediate forms occur, it is the opinion of the author that this plant should be considered a distinct geographical variety rather than a species.

ATHYRIUM ALPESTRE (Hoppe) Rylands ex Moore var. **americanum**, var. nov., omnibus frondium segmentis iisdem formae typicae angustioribus, inter se plus distantibus ultimis linearibus, soris minutis (0.5–0.7 mm. latis) rotundis submarginalibus, soris singulis dente marginali pinnulae everso tectis, velo nullo.

This variety is found in subarctic and high alpine situations from Alaska and British Columbia to California and Colorado, also in Gaspé Co., Quebec.

The following specimens of *Athyrium alpestre* var. *americanum* are in the Gray Herbarium:

QUEBEC: forming extensive areas in the alluvium of alpine brooks, easterly and northerly slopes, Table-top Mt. Gaspé Co., August 9, 1906, *Fernald and Collins* no. 151a; (specimens 9 dm. tall; crevices of granite rock, altitude 750–1050 m., easterly and northerly slopes Table-top Mt. Gaspé Co., August 9, 1906, *Fernald and Collins* no. 151.

MONTANA: altitude 5500–6000 ft., Glacier Basin below Sperry Glacier, August 5, 1901, *F. K. Vreeland* no. 1058.

IDAHO: moist places, Packsaddle Peak, Kootenai Co., August 6, 1892, *Sandberg, McDougal and Heller*, no. 858.

WYOMING: in glacial drift, Teton Mts., July 26, 1901, *Merrill and Wilcox* no. 1032.

COLORADO: rocky slopes and rock crevices, summit of North Park Range, Larimer Co., August 10, 1903, *L. N. Goodding* no. 1841.

CALIFORNIA: near summit of Mt. Rose, 8600 ft. altitude, 1877, *J. G. Lemmon* no. 1160; 7500 ft. altitude, Mt. Shasta, August 17, 1881, *C. G. Pringle*; 7800 ft. altitude, Mt. Shasta, August 16, 1903, *E. B. Copeland* (distributed by *C. F. Baker*) no. 3917; Mt. Shasta, 1877, *Hooker and Gray*; Mt. Shasta, 1897, *W. M. Canby* no. 414.

WASHINGTON: loose rock, 6000 ft. altitude, Mt. Rainier, August, 1895, *C. V. Piper* no. 2111; Mt. Rainier, August 1890, *E. C. Smith*.

BRITISH COLUMBIA: mountains near Ainsworth, Kootanie Lake, altitude 6000 ft., July 10, 1890, *John Macoun*; altitude 5500 ft., Fish Creek Valley, August 1906, *Butters and Holway*; on dry rocks, near top of Mt. Cheops [near Glacier], altitude 8200 ft., July 12, 1904, *E. R. Heacock* in *Shaw's Selkirk Flora* no. 453; altitude 4400 ft., Rogers Pass, August 23, 1904, *E. R. Heacock* in *Shaw's Selkirk Flora* no. 554; Selkirk Range, August 24, 1885, *John Macoun*; Cascade Mts. 49° N. lat., 1859, *Dr. Lyall*.

ALASKA: mountains, interior of Unalaska, October 10, 1871, *M. W. Harrington*.

The following specimens approach close to the European form in the cutting of the frond, but have no indusia:

CALIFORNIA: near summit of Sierra Nevada, Nevada Co., 1873, *Miller*; ridge south of Donner Pass at 7500 ft., Nevada Co., August 17, 1903; *A. A. Heller* no. 7186; 11500 ft. altitude, Saw Tooth Peak, Tulare Co., August 17, 1904, *Culbertson*.

OREGON: Union Co., 1878, *W. C. Cusick*.

WASHINGTON: Wenatchie region, altitude 7000 ft., August 1883, *T. S. Brandege* no. 1222.

From this study of the *Filix-femina* group of *Athyrium*, it appears that these ferns follow certain laws of distribution, which have been noted often in the case of Phanerogams. Thus we find that the common woodland species of eastern North America (*A. angustum*) either reappears in eastern Asia, or is represented there by a very closely related species.¹ This plant, like many others of eastern North America ranges northeastward into the region of the Gulf of St. Lawrence, and there appears, often in a peculiar form, the variety *laurentianum*.² A very distinct species (*A. asplenoides*) occurs in the southeastern United States, and like so many plants of that region, extends northward along the Atlantic as far as southeastern New England.

The common fern of cool temperate Europe (*A. Filix-femina*) extends well across Asia, occurs in Kamchatka, and reappears in Alaska and British Columbia in precisely the same form. There are, however, in each of the chief areas occupied by this species, certain well marked minor forms peculiar to the respective regions,—in Europe the various finely cut forms, especially that commonly known as the variety *rhaeticum*, in the Pacific coast region from Alaska to Oregon the variety *sitchense*. Like a great number of plants of the wet western coast, this latter variety reappears at low altitudes on the climatically similar west slope of the Selkirk Range.³

¹ The close relations between the flora of the region of deciduous forests of eastern North America and the corresponding region of eastern Asia, was long ago pointed out by Asa Gray, in his classic essay, "Observations upon the Relation of the Japanese Flora to that of North America and other Parts of the northern Temperate Zone." *Mem. of the Am. Acad. of Arts and Sciences*, vi. 377 (1859).

² Professor Fernald, in studying the flora of the region about the Gulf of St. Lawrence, has found that a great many of the plants of that region are similarly peculiar. He informs me that it is never safe to assume that a plant of Newfoundland or Gaspé is identical with an apparently similar species of the eastern United States, until a detailed study has been made of all its technical characters.

³ Several years ago the author pointed out (*The Vegetation of the Selkirk Mountains*, Appendix A. to Howard Palmer's "Mountaineering and exploration in the Selkirks" 354, 1914)

The southern extension of *A. Filix-femina* into the western United States is marked by a peculiar technical variety, as seems often to be the case with northern plants which extend south into California and the southern Rocky Mountains.

The *Filix-femina* group of the genus *Athyrium* presents a typical case of boreal distribution. Apparently the center of this distribution is somewhere in Asia. Christ says of the genus *Athyrium* in China, "The variation of the genus *Athyrium* in southern China is only equalled by that of the same genus in Japan and the Indian Himalaya, other countries belonging to the same botanical region. . . . It is a plastic mass which appears to be endlessly modified."¹

On the other hand the number of species of this genus in North America is limited to those just described and the two diplazioid species *A. acrostichoides* and *A. angustifolium*.

Moreover, as has been pointed out already, the *Diplazia* of tropical America, presumably descendents from the genus *Athyrium*, though very numerous as to species, appear to belong almost wholly to a section of the genus which is probably descended from *Athyrium acrostichoides* (Sw.) Diels or some very similar species, while the Asiatic *Diplazia* form a mass of species of almost endlessly complicated relationships.

Athyria of the true *Filix-femina* group extend south into the tropical mountains in Mexico (*A. Martensi* and *A. Dombei* Desv.), and

the strong relationship of the boreal flora of the Selkirk Range with that of Scandinavia. Evidence is accumulating, that this relationship extends to parts of the flora which cannot be considered as arctic-alpine, but rather cool temperate and subalpine.

The lady fern is only one of numerous cases in which plants of cool temperate Europe occur, in precisely the same form, in the cool and moist evergreen forests of British Columbia and Alaska.

The occurrence of *Athyrium alpestre* in the mountains of western America,—in this case in a somewhat modified form,—is another instance of the relationship of European and north-west American floras, though in this case the plant is distinctly alpine in character. The further extension of its range to the Gaspé region is entirely in keeping with the known facts concerning the flora of that interesting region. See Fernald, M. L., *The Soil Preferences of Certain Alpine and Subalpine Plants*. RHODORA, ix. 149 (1907).

The Reappearance of the variety *sitchense* in the western part of the Selkirk Range, is also entirely normal. Piper, in his *Flora of Washington*, Contrib. from the U. S. National Herb. xi. 53 (1906) called attention to the large number of west coast plants, which do not occur in the interior of Washington, but which reappear in the more moist hill country of eastern Washington and northern Idaho. Evidence is accumulating that a much larger number of coastal forms occur farther north in the region around Revelstoke, the interior region, which, above all others, has the nearest approach to the coastal climate.

¹ La variation du genre *Athyrium* en Chine mérid. n'a d'égale que celle du même genre au Japon et l'Himalaya indien, pays du reste qui appartient à la même région botanique. . . . C'est une masse plastique qui semble se modifier sans cesse. Christ, H. Les collections de Fougères de la Chine au Museum d'histoire naturelle de Paris. Bull. Soc. Bot. de France lii. Mém. i. 50 (1905).

thence into the South American Andes, in India (*A. pectinatum* Pr.) and in Abyssinia (*A. Schimperii* Mong., apparently the closest relative of our *A. asplenoides*). With these exceptions they are entirely wanting from the tropical regions, and from the southern hemisphere.

II. BOTRYCHIMUM VIRGINIANUM AND ITS AMERICAN VARIETIES.

In 1915 Fernald and St. John¹ called attention to the fact that *Botrychium virginianum* about the Gulf of St. Lawrence differs from the more southern typical plant in several respects. They identified this form with *Botrychium virginianum* var. *europaeum* Ångström, a rare fern of Scandinavia, Russia, and central Europe. A re-examination of all the North American and European material of this species in the Gray Herbarium indicates that the actual condition is somewhat more complex.

In this examination particular attention has been paid to the character of the sporangia and of the ultimate segments of the fertile frond which bear the sporangia.

Each of the varieties has, indeed, its own characteristic sterile frond, but the attempt to distinguish them on this ground is unsatisfactory in view of the slight and often scarcely describable differences between the fronds of the different varieties, and the very considerable individual variation within the same variety.

Typical *Botrychium virginianum* (L.) Sw. has a sterile frond of thin texture with the pinnules lanceolate, deeply pinnatifid or nearly pinnate, and the ultimate segments oblong or lanceolate and scarcely or not at all spatulate. The ultimate segments of the fertile shoot are narrow (0.25–0.5 mm.) and thick, and in dried specimens appear nearly opaque. The mature sporangia are dark in color, varying in different plants from a moderately dark yellow brown to almost black. As in all the species of *Botrychium*, they vary considerably in size, the largest measuring 0.5–0.8 mm. in length and somewhat less in width.²

¹ Fernald, M. L., and St. John, Harold, The Occurrence of *Botrychium virginianum* var. *europaeum* in America. RHODORA, xvii. 233 (1915).

² The measurements of sporangia given throughout this discussion of *Botrychium virginianum* and its varieties, are all taken from large fully developed sporangia. Smaller sporangia are always mingled with the large ones, and these vary in size in the respective species proportionally with the larger ones.